Asian Eden

Large herbivore ecology in India

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Asian Eden

Large herbivore ecology in India

Farshid S. Ahrestani

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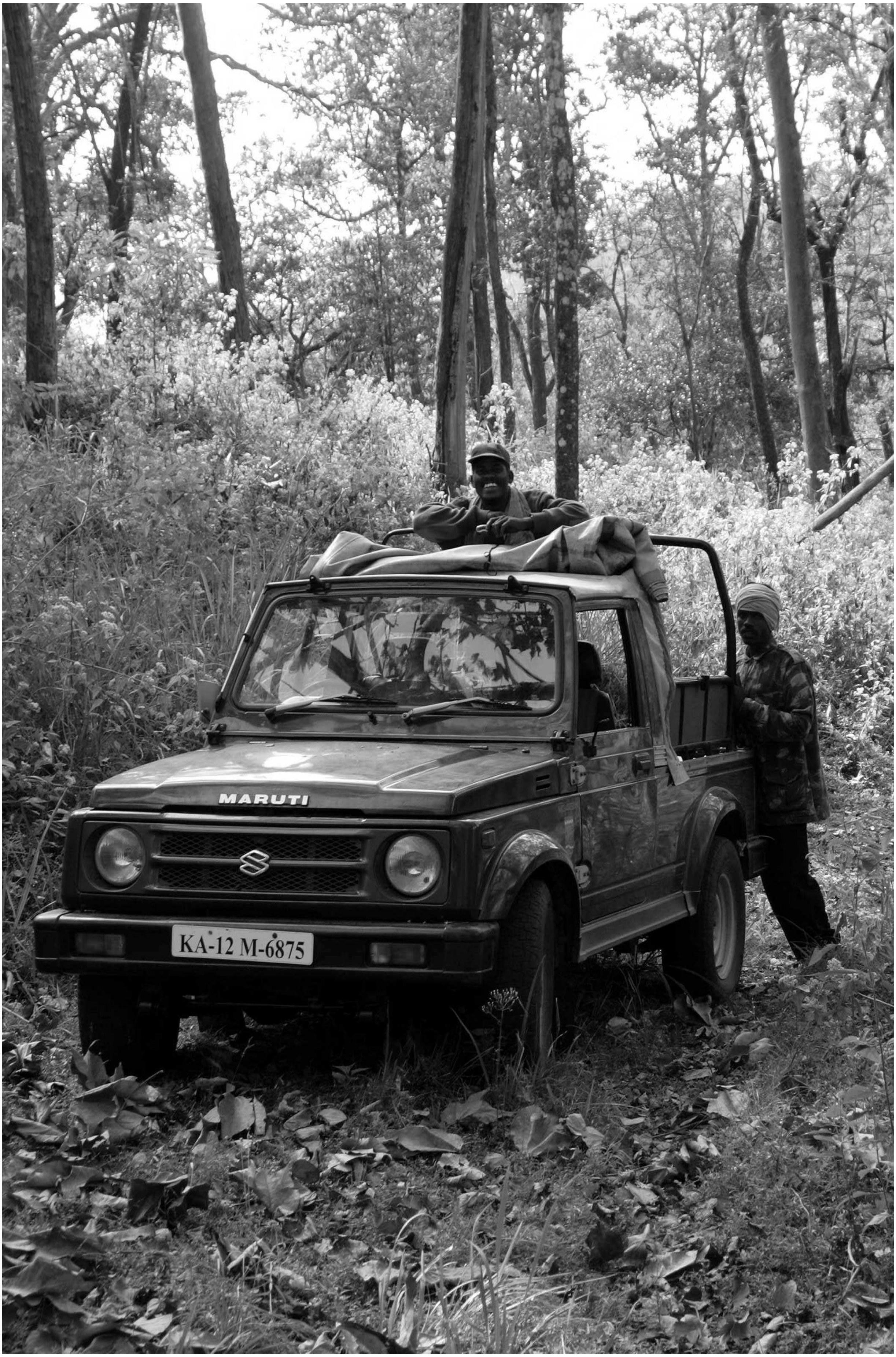
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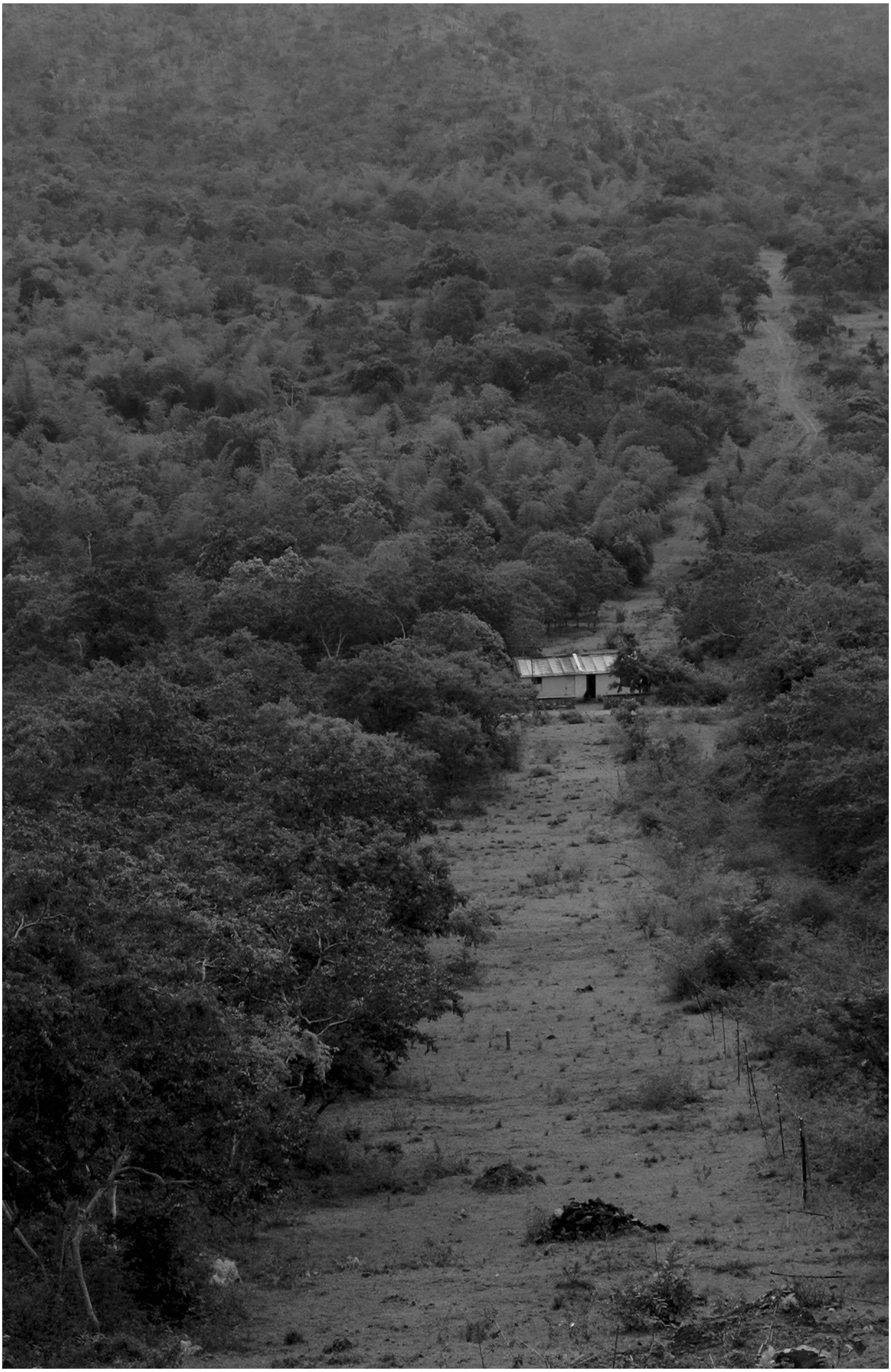
Abstract

The study of large mammalian herbivore ecology has a strong allometric tradition. The majority of studies that have helped better understand how body mass affects large herbivore ecology in the tropics, from a biological, functional, and ecological perspective, are from Africa. India’s large herbivore assemblage—the richest outside of Africa and with a body mass range similar to Africa’s—is a poorly understood assemblage that has never been studied from the perspective of body mass theory. The goal of this study was to bridge this gap. I tested hypotheses of large herbivore biology and ecology in India based on body mass theory across different spatial, temporal and organizational scales. Data collection and analyses included: a 20 month field study the provided data of forage availability, the seasonal variation in diet, habitat preference and overlap, the timing of parturition, and the *life history* traits of different body mass large herbivore species in South India; a year long treatment based exclosure field experiment that provided a better understanding of the seasonal variation in graminoid biomass and quality in South India; a country level analysis of the distribution of the large herbivore assemblage with respect to environmental covariates; and a modelling approach to determine the impact of body mass on reproductive biology. Results showed that body mass based principles offered explanations for some, but not all, of what I observed and predicted. This study for the first time proposes that the impact of body mass might explain why some smaller herbivore species show seasonality in annual parturition while some large herbivores species do not. Also, as predicted and similar to Africa, large herbivore species richness in India is highest in areas with high soil nutrients and intermediate moisture levels. Beyond this study, important questions that still remain are “Which environmental and ecological conditions shaped species richness in Africa to be four times higher than what is found in India?” As India remains the last stronghold—Asia’s Eden—for most of Asia’s large herbivores, there is a need for further studies of the biology and ecology of large herbivore species in India.



1

General introduction

Farshid S. Ahrestani

Large mammalian herbivores

Large mammalian herbivores are an ubiquitous and prominent guild of species. The 260+ large mammalian herbivore species in the world occupy a wide range of habitats including deserts (for example, scimitar-horned oryx *Oryx dammah* and Asiatic wild ass *Equus hemionus*), tundra (for example, reindeer *Rangifer tarandus* and musk ox *Ovibos moschatus*), and tropical forests (for example, barking deer *Muntiacus muntjak* and pudu *Pudu pudu*). Some large herbivore species are rare and have restricted ranges, like the saola *Pseudoryx nghetinhenisis* (described by science less than a decade ago and believed to be found only in Laos and Vietnam) and the mountain anoa *Bubalus quarlesi* (Sulawesi, Indonesia), while other species have a wide range, like the Barbary stag/ wapiti/red deer/maral/hangul *Cervus elephus* (North Africa, Europe, Asia, and North America). Large mammalian herbivores have the largest body size range among terrestrial animals, from 5 kg duikers *Cephalophus spp*. to 5,000 kg African elephants *Loxodonta africana*.

The bulk of radiation of large mammalian herbivores is understood to have occurred in the Pliocene – Pleistocene (5.3 mil – 50,000 BP) and by the mid Pleistocene (approximately 30 – 50,000 BP) large herbivore species dominated ecosystems worldwide (Owen-Smith, 1987). During the late-Pleistocene (10 – 30,000 BP), however, over 75% of these species became extinct in North America, 45% in Eurasia, and 14% in Africa. There is still no clear consensus on whether climate change (Trueman *et al*., 2005; Johnson, 2002, 2009) or the impact of humans (Prins, 1998; Koch & Barnosky, 2006) was responsible for this species loss. Today, among the continents, Africa has the richest assemblage of large herbivores species.

Large herbivores have been providing food, fibre, draught and fertiliser for human populations for more than 500,000 years (Roth & Merz, 1997; Gordon, 2009). They were also one of the first wild animals to be domesticated, a process that began 9 – 10,000 years BP (Clutton-Brock, 1992; Roth & Merz, 1997). Today, large herbivores are the major source of protein for multiple societies (Loibooki *et al*., 2002; Milner-Gulland & Bennett, 2003); an important component of the socio-economics of many human societies (Prins *et al*., 2000; Gordon *et al*., 2004); and are important for nature conservation not only for their ecosystem services, but also for their ability to draw tourists and raise money for conservation (Barnes *et al*., 1999; Prins *et al*., 2000).

Besides their importance to human society, large herbivores are an integral and important component of most terrestrial ecosystems (Scholes & Archer, 1997; Dharani *et al*., 2008; Dobson, 2009). Large herbivores often impact ecosystems, which includes modifying structural diversity of savannas with respect to total vegetation cover and woodland encroachment (Prins & Van der Jeugd, 1993; Dublin, 1995; Asner *et al*., 2009; Hagenah *et al*., 2009); reducing the incidence of fire with the removal of flammable biomass (McNaughton *et al*., 1988; Van de Vijver *et al*., 1999); regulating nutrient recycling via the input of faeces and urine (McNaughton *et al*., 1997; Augustine, 2003); and modifying vegetation community structure (Milchunas *et al*., 1988), species fitness (Wise & Abrahamson, 2007), composition (Augustine & McNaughton, 1998), biomass production (McNaughton, 1976), and seedling survival (Goheen *et al*., 2004). Large herbivores also impact the ecology of other animals, including carnivores (Sinclair *et al*., 2003), birds (Milchunas *et al*., 1998), and arthropods (Gonzalez-Megias *et al*., 2004).

Free ranging large herbivores having disappeared from many parts of Africa (Prins, 1992; Lamprey & Reid, 2004) and Asia. Currently some large herbivore species are threatened with extinction (like the saola and mountain anoa) and many rich and diverse large herbivore assemblages face the threat of species extirpations (Du Toit & Cumming, 1999). It is important that the richness and diversity of large herbivores species be maintained, as species of different body mass are known to have different ecosystem functions (Bakker *et al*., 2004; Hobbs & Searle, 2005). There is, therefore, a need to conserve these species. In order to effectively conserve, however, we first need to understand the biology and ecology of these species.

Large mammalian herbivore ecology and coexistence

Gause (1934) made one of the earliest propositions regarding species coexistence stating "that two species with similar ecology cannot live together in the same place". By the late 1950s Hardin had formalized this into the Competitive Exclusion or Exclusion principle which basically contended that "complete competitors cannot coexist". At the same time Hutchinson (1957) proposed the (complementing) niche concept. Although predation pressures (Sinclair *et al*., 2003) and disease susceptibility (Dobson & Hudson, 1986) have been proposed as being important 'niche' dimensions for a large herbivore species, it is accepted that forage resource partitioning is the main driver of their coexistence.

Vesey-FitzGerald's (1960) observations of 'ecological succession' and Lamprey's (1963) observations of 'ecological separation' among large herbivores were some of the first propositions defining how large herbivores coexist. Within a decade, there were multiple landmark studies that proposed both complementing as well as conflicting hypotheses of how species partition their resources: Bell (1969) and Jarman (1973) proposed that coexistence of large herbivores can be explained as a function of species body mass and digestive physiologies; while Hofmann and Stewart (1972) proposed that a herbivore's diet was determined only by its digestive physiology. Despite Hofmann's (1989) reiteration of his hypothesis, as Belovsky (1997) pointed out "the study of foraging by mammalian herbivores has had a long-standing allometric tradition." The Jarman-Bell principle (Geist,1974)—which proposed that large body mass herbivore species can survive on foods of lower nutritional value than smaller body mass species—remains at the core of this allometric tradition.

The mechanism that explains the Jarman-Bell principle is the combination of the ¾ exponential allometric function of a species metabolic rate (Kleiber, 1932) and the linear allometric function of their gut capacity (Demment & Van Soest, 1985). Although Kleiber's sample size was small, his proposition has held up to recent intense scrutiny (Darveau *et al*., 2002; Enquist *et al*., 2003; Da Silva *et al*., 2006). Large herbivores are either foregut—the strategy that dominates the guild—or hindgut fermenters. These digestive physiologies have been well studied (particularly ruminants: Van Soest, 1994), they still continue to receive attention (Clauss *et al*., 2003; Perez-Barbaria *et al*., 2004; Hummel *et al*., 2006; Edouard *et al*., 2008), and the linear allometric function of gut capacity is still accepted (Prins & Van Langevelde, 2008).

While assuming the Jarman-Bell principle to be true, an impressive number of studies have helped us better understand the ecology of large herbivores in relation to their biotic and abiotic environments. Among the abiotic parameters, the impact of available moisture, available soil nutrients, and fire have received the most attention because of their importance for the variation in forage production and quality (Coe *et al*., 1976; Van Langevelde, *et al*., 2003). The spatial variation of these abiotic resources has been shown to explain the spatial variation in large herbivore richness and diversity (Olff *et al*., 2002; Klop & Prins, 2008). We also now better understand how species exploit the variation of forage resources along a temporal scale, seasonally (Bell, 1970; Prins & Beekman, 1989) as well as multiple year (Vesey-FitzGerald, 1960; McNaughton & Geogidis, 1986); and along a spatial scale, complex local landscapes (McNaughton, 1985; Fryxell *et al*., 2005) as well as large migratory scale landscapes (Wilmshurst *et al*., 2000; Boone *et al*., 2006). Studies have shown that the variation in plant species (Jarman, 1973; Hansen *et al*., 1985; Perrin & Brereton, 1999), plant structure (Farnsworth *et al*., 2002; Drescher *et al*., 2006) including variables like plant height and leaf-stem ratio (Voeten & Prins, 1999; Drescher *et al*., 2006), and sward density (Murray & Illius, 2000) can all affect large herbivore foraging.

Large herbivore ecology has also been investigated from a functional point of view (Prins & Olff, 1998) and optimal foraging theory has been adequately applied to its foraging ecology (Belovsky, 1997). Also, the stability of large herbivore-vegetation systems has been studied (Owen-Smith, 2002) as well as the stability of large herbivore populations (Illius & O'Connor, 2000; Owen-Smith, 2004). Although recent studies have looked at how resource competition might shape *life history* traits of large herbivores (De Roos *et al*., 2009), empirical data is still lacking to conclusively show competition between large herbivore species (Arsenault & Owen-Smith, 2002).

All the above studies cited are from Africa. Remarkably not one study of India's large herbivore assemblage—with a body mass range similar to Africa's and the richest outside of Africa—has explored the importance of the impact of Jarman-Bell principle on its species and community ecology. This study aims to fill that gap within the context of what we know from climatically similar tropical Africa.

Outline of thesis

Since the seasonal variation in plant biomass and quality are key parameters of large herbivore diet and foraging ecology, in Chapter 2 **Seasonal variation in herbaceous biomass and nitrogen content in South India: implications for large herbivores** I present and discuss results of a field-based plant growth experiment that I conducted in South India. The goals of this experiment were to quantify the seasonal variation in the availability of graminoid biomass and nutrients, determine whether graminoid production was limited by water and/or nitrogen, and discuss the impact of these variations on local large herbivore foraging ecology. The results from the experiment enabled comparison of environmental conditions in other tropical areas in the world that support large herbivore assemblages.

Understanding how species partition resources to coexist is integral to understanding large herbivore foraging ecology. In Chapter 3 **The role of body mass in diet and habitat selection by large herbivores species in a tropical South Indian forest** I investigate the seasonal variation in diet, habitat preferences, and niche breadth of large herbivore species of different body mass and digestive strategy, i.e., three ruminants species (the 65 kg chital *Axis axis,* 205 kg sambar *Cervus unicolor*, and 730 kg gaur *Bos gaurus*) and a large hindgut fermenter (3120 kg Asian elephant *Elephas maximus*). The study was conducted in Bandipur and Mudumalai National Parks, South India, in a landscape that included dry and moist deciduous tropical forests with seasonally variable forage quality. The mail goal of this study was to see whether body mass based principles would explain observed inter-species differences of diet, habitat preference, and niche breadth and overlap.

I observed during my field work that chital and gaur had different annual parturition patterns. Chital parturition appeared to be timed with the period of highest plant quality, while gaur parturition occurred throughout the year. In Chapter 4 **Why some species time their annual parturition with high plant quality availability? - the impact of body mass** I investigate whether the difference in body mass between chital and gaur could explain why the species had different annual timing of their parturition. I use results from the experiment in Chapter 2 to calibrate a model that I developed to track the seasonal variation in graminoid production and nutrients. I combine the results of the model along with our understanding of the allometric functions of nutritional requirements of a species to try and find support for my proposition that the impact of body mass can explain the difference between the parturition of chital and gaur.

Body mass has been shown to be a significant correlate of species *life history* traits. The gaur—Asia's largest ruminant species, the world's largest bulk feeder—is a vulnerable and poorly understood species. I conducted a study of India's largest gaur captive population at Mysore Zoo to better understand **Age and sex determination of gaur *Bos gaurus*** (Chapter

5). The interesting body mass status of the gaur—at the megaherbivores-mesoherbivores divide—prompted me to use the results from Chapter 5 to undertake Chapter 6 the **First detailed analysis of life history traits of the Asian megaherbivore, gaur *Bos gaurus***. I compare my analysis of gaur *life history* traits with that of other similar body mass and phylogenetically related Bovinae species like African buffalo *Syncerus caffer*, North American bison *Bison bison*, and banteng *Bos javanicus*.

Scaling up spatially, I was interested in investigating whether the two most important plant production parameters, available moisture and soil nutrients, have the potential to explain large herbivore species distribution patterns at a regional scale in India. Therefore, in Chapter 7 **Determinants of large herbivore diversity in sub-Himalayan India**, I present analyses of the distribution of the 16 large herbivore species in sub-Himalayan India in relation to the distribution of available moisture and soil nutrients.

In the last chapter, Chapter 8 **Body mass and large herbivore ecology in India: a synthesis**, I synthesize results from Chapters 2 – 6 within a theoretical framework. I also correlate findings between chapters and discuss what lessons were learnt, the new questions that were raised, and old debates that were revived.

Study site

The field study site (N $11^{o}32^{'}$-$41^{'}$, E $76^{o}22^{'}$-$41^{'}$) (Chapters 3, 4, 5) was spread over two contiguous National Parks in South India, Mudumalai in the state of Tamil Nadu and Bandipur in the state of Karnataka (Fig. 1.1). Both these National Parks are part of the large Nilgiri Biosphere conservation area and are located in the lower to middle elevation region of the Western Ghats, which has undulating terrain 250 – 1400m. The rainfall is monsoon driven, annual average was 955mm in the east (1977 – 2007) and 1240 mm in the west (1991 – 2006). There are three primary seasons: a Southwest monsoon wet (May-July: 60% of rainfall), a Northeast monsoon wet (August – November: 40% of rainfall) and a dry (December – March). The data to determine niche breadth and diet composition in Chapter 3 were collected from an area of 400 km^{2} that included the 255 km^{2} area used to collect chital and gaur demography data (Chapters 4 & 6).

The study site has an east-west moisture gradient (the east being dry) which has resulted in dry deciduous forests in the east (*Boswellia serrata- Anogeissus latifolia-Acacia catechu-Terminalia tomentosa-Terminalia paniculata-Albizzia camara-Cassia fistula-Dalbergia latifolia-Stereospermum personatum-Diospyros montana*), and moist deciduous forests in the west (*Boswellia serrata-Anogeissus latifolia-Terminalia tomentosa-Terminalia bellirica-Dalbergia latifolia-Pterocarpus marsupium-Shorea talura*. The extreme east is thorn-scrub (*Acacia planifrons-Balanites roxburghii-Capparis spp.-Prosopis spp.-Azadirachta indica-Diospyros chloroxylon-Phoenix sylvestris*) and the extreme west is semi-evergreen forests (*Olea dioica-Toona ciliata-Glochidion velutinum-Elaeocarpus tuberculatus*). The study site's understory (particularly in the dry deciduous region) is dominated by non-native invasive species—primarily *Lantana camara* and *Chromolaena odorata*, and to a lesser extent *Parthenium hysterophorus*—that not only have displaced palatable grasses but are also not preferred forage for large herbivores.

The recent trend of exotic invasives increasingly dominating land cover has the potential to impact the study site's large herbivore mammalian species biomass carrying capacity, currently the highest in Asia and comparable to high large herbivore biomass areas in Africa as well (Karanth, 1992). Seven species of herbivores occur in the study site, the tiny 4-5 kg mouse deer (*Moschiola meminna*), followed by the four-horned antelope (*Tetracerus quadricornis*), barking deer (*Muntiacus muntjak*), chital (*Axis axis*), sambar (*Cervus unicolor*), gaur (*Bos gaurus*) and Asain elephant (*Elephas maximus*). High densities of the rich herbivore assemblage means that the study site is an important conservation area for the future of the tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*).

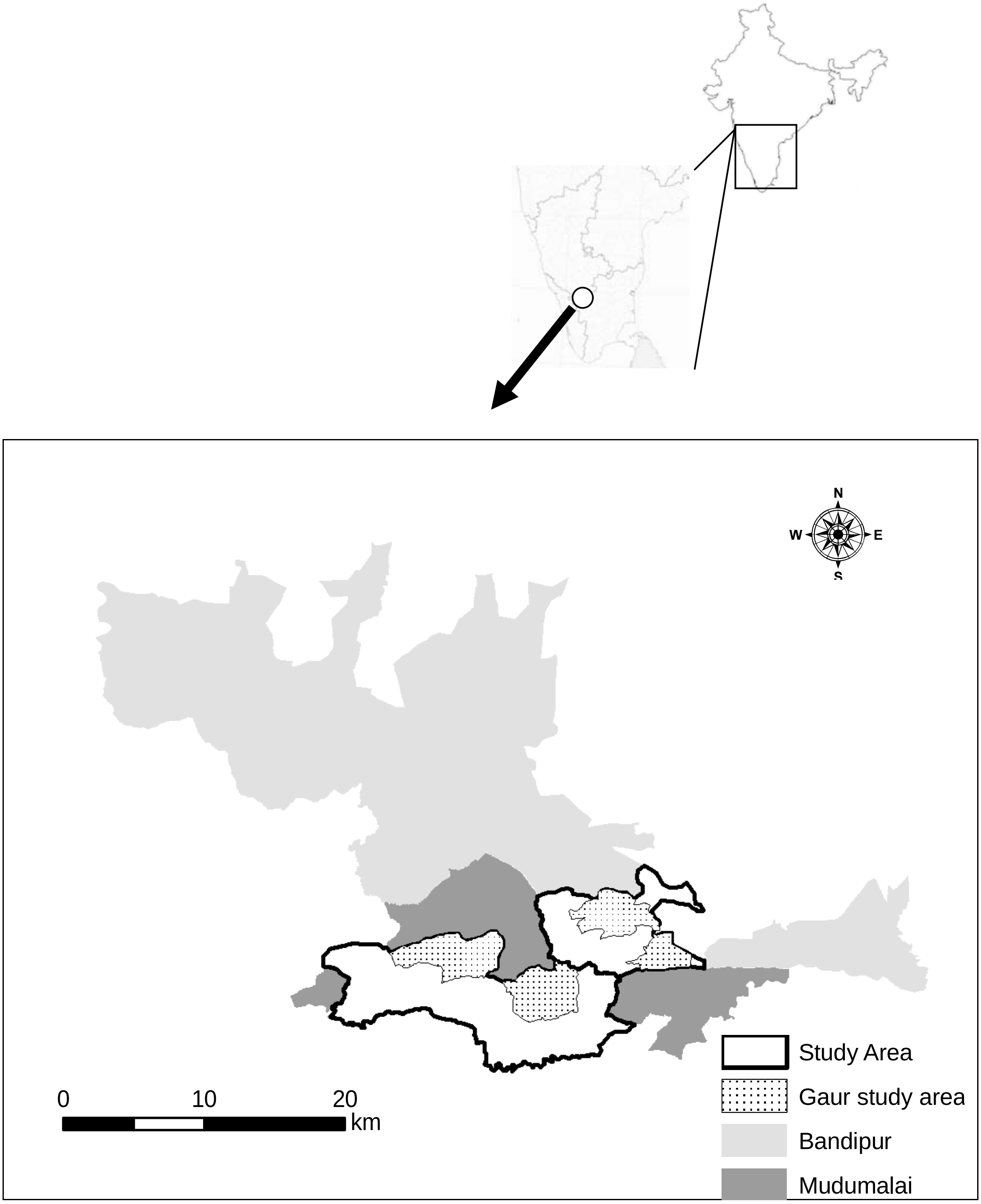


Fig. 1.1. Field study site

Table 1.1. Large herbivores found in Sub-Himalayan India and their weights. Species in bold were studied in the field.

Common name	Scientific name	Body mass (kg)	References
Asian elephant	***Elephas maximus***	**3120**	**6,12,13**
Indian rhinoceros	*Rhinoceros unicornis*	1800	5,6,8,13
Gaur	***Bos gaurus***	**730**	**8,10**
water buffalo	*Bubalus arnee*	700	5,8,13
Indian wild ass	*Equus hemionus*	240	3,5,8,13
Sambar	***Cervus unicolor***	**205**	**1,2,7,10**
Nilgai	*Boselaphus tragocamelus*	195	11
swamp deer	*Cervus duvauceli*	170	5,8,10,13
Nilgiri tahr	*Hemitragus hylocrius*	90	5,16
wild pig	*Sus scrofa*	80	9
spotted deer (chital)	***Axis axis***	**65**	**4,10,13**
hog deer	*Axis porcinus*	42	5,8
Blackbuck	*Antilope cervicapra*	29	9
Muntjac	*Muntiacus muntjak*	24	8,13
four-horned antelope	*Tetracerus quadricornis*	19	8,13
Indian gazelle (chinkara)	*Gazella bennettii*	17	5,13

References: 1. Crandall (1964); 2. Downes (1983); 3. Foose (1982); 4. Geist & Bayer (1988); 5. Hutchins (2004); 6. Laurie (1982); 7. Lydekker (1916); 8. Macdonald (2006); 9. Mungall (1978); 10. Schaller (1967); 11. Sheffield *et al*. (1983); 12. Shoshani & Eisenberg (1982); 13. Walker (1999)

2

Seasonal variation in herbaceous biomass and nitrogen content in South India - Implications for large herbivores

Farshid S. Ahrestani, Ignas M.A. Heitkönig and Herbert H.T. Prins

Abstract

We present results from a nitrogen and water treatment exclosure field-based experiment that assessed the seasonal pattern of biomass and nitrogen content and determined the limiting factors of graminoid production in the herbivore rich Western Ghats region of South India. We found graminoid production to be nitrogen limited, and despite below average annual rainfall, additional water did not significantly increase biomass production. Graminoid leaf nitrogen content levels were low relative to other tropical areas, implying low plant quality availability for grazers. As predicted, leaf nitrogen levels were highest in the early wet season (April-May) and then decreased monotonically reaching their lowest levels in the late dry season. The growing season spanned the entire rainy season and ceased in the dry season, resulting in accumulated standing biomass being the highest in late wet/early dry season (December-January) and lowest in the dry season. The dry season, therefore, is period in the year that poses the greatest challenge for grazers with respect to both graminoid biomass and its nitrogen content. Grazing appeared to have a positive effect on green grass production; the growing season of graminoids was longer in grazed than in ungrazed plots. Finally, while biomass production is the study area was similar to other tropical areas in the world, the relatively low graminoid nitrogen levels in the region posses a challenge to large herbivores, particularly smaller body mass species and lactating females.

Introduction

The herbaceous layer is a key forage component to many large herbivores and the spatial and temporal variation of its quantity and quality affects large herbivore biology, ecology, and species diversity (Mattson, 1980; Beever *et al*., 2000; Prins & Van Langevelde, 2008). The variable availability of herbaceous biomass and quality suggests that the impact of resources varies in different regions and herbivore populations. This variation is best illustrated by: the timing of parturition in multiple populations of large herbivore species coincides with the season of highest plant quality (Rutberg, 1987); the mass migration of herbivores (like in East Africa's Serengeti-Mara ecosystem) is recognized as being a function of herbivores tracking spatiotemporal variation in plant quantity and quality (Vesey-Fitzgerald, 1960; Bell, 1970; Frank *et al*., 1998; Boone *et al*., 2006); and large herbivore species diversity patterns in East and West Africa correlate to the spatial distribution of the availability of herbaceous quantity and quality (Coe *et al*., 1976; Olff *et al*., 2002; Klop & Prins, 2008).

In Africa—a region where the herbaceous layer is a resource component supporting the world's richest and most diverse large herbivore assemblage—it has been shown that it is necessary that the phenology of the herbaceous layer, and what affects its biomass and quality, be understood in order to comprehend herbivore ecology (Coughenour, 1985a,b; Prins, 1988; Prins & Loth, 1988). India supports a rich and diverse large herbivore species assemblage, of which many are grazers (Prater,1985). Studies have investigated herbaceous layer production in North India and have shown that its biomass is relatively high when compared to other tropical regions and that production was affected by available moisture and grazing (Pandey & Singh, 1991, 1992). North India (excluding the dry Western region) and South India do not differ significantly with respect to rainfall, but North India is richer in soil nutrients as a function of the constant replenishment of rich alluvial soil from multiple rivers originating in the Himalayas. Results from North India, therefore, may not necessarily be applicable for South India. Importantly, thought, there exists little understanding of herbaceous production in South India in the context of herbivore forage requirements.

Globally, the two most limiting factors of herbaceous layer (graminoid) production are the moisture and soil nutrients (Pandey & Singh, 1992; Hopkins, 2000). Both the amount and the temporal (seasonal as well as annual) variation in moisture availability affect graminoid growth (Le Houérou *et al*., 1988; Milchunas *et al*., 1994, 1995), and from among the list of soil nutrients necessary for graminoid production, nitrogen stands out as being the most important (Chapin, 1980; Parsons & Chapman, 2000).

To help better understand large herbivore ecology in South India, we conducted a nitrogen and water treatment exclosure field-based experiment in the herbivore rich Western Ghats region to 1) assess the seasonal pattern of biomass and leaf nutrient content, and 2) determine what limits graminoid production in South India. Also, based on knowledge from other tropical regions with cyclic water availability (Menaut & Cesar, 1979; Breman & De Wit, 1983; Deshmukh, 1986; Prins, 1988; Kamnalrut & Evernson, 1992; Bacon, 2004) we predicted that 3) leaf nitrogen content would peak in the early wet season, then continuously decrease till its lowest level in the dry season, and 4) graminoid production would not be extended by water availability in the dry season.

Methods

Experiment design

We conducted a field experiment (August 2006 – July 2007) on a grassy meadow that was located in a wildlife resort (1076 m) bordering the Nilgiri Biosphere, South India (N 11^{o}55’, E 76^{o}63’). The Nilgiri Biosphere hosts a diverse assemblage of herbivores including Asian elephant (*Elephas maximus*), gaur (*Bos gaurus*), sambar (*Cervus unicolor*), chital (*Axis axis*), muntjac (*Muntiacus muntjak*), four-horned antelope (*Tetracerus quadricornis*) and Indian spotted chevrotain (*Moschiola meminna*). The study site receives a monsoonal driven rainfall cycle that includes a wet (May – November) and a dry (December – April) season. The wet season is bimodal in nature as two sources contribute to the precipitation received: the Southwest monsoon (May – July) followed by the Northeast monsoon (September – November). The rainfall during our 12-month study period was 730 mm (Fig. 2.1) (recorded in Masinagudi 2 km north of the experiment site), which was below a previous 15 year (1991-2005) average of 860 mm. Mean monthly temperature was 24^{o}C, reaching a high of 34 – 35^{o}C in April – May and a low of 5 – 6^{o}C in December-January. We found the soils at the experiment site to be slightly acidic (5.02 ± 0.14 95% CI, n = 5) and low in nitrogen content (0.12 ± 0.07% CI, n = 5). The soil surface was sandy loam and had a gravelly clay substrate.

The design included watering and fertilization in grazing-protected plots that were located within five fenced exclosures (7.5x4.5 m) that excluded large herbivores but not rodents and hares. Historically the fenced plots had been grazed by cattle and wild herbivores. Each of the five exclosures contained nine 2x1 m treatments plots (inter-plot spacing was 0.5m) of a fully factorial 3x3 (three treatment levels of two factors) design arranged in a randomized block design. The three treatment levels of the two factors were: 1) moisture, with levels (a) no additional water (control), (b) addition of 300mm/m^2 spread over the wet season, treated in equal parts every three days, (c) addition of 300mm/m^2 spread over the entire year, treated in equal parts every three days; and 2) nitrogen (added in the form of NH_4NO_3), with levels (a) no addition of N (control), b) addition of 7g N m^{-2} yr^{-1}, and c) addition of 21g N m^{-2} yr^{-1}. The quantity of 300mm (the difference between annual average and wettest year) was used to simulate a wet year. The nitrogen (NH_4NO_3) treatments were applied in three dosages over the growing season: 25% on June 25, 50% on August 23, and 25% on October 3 2006. Samples (n = 5 for each treatment on each sampling occasion) of above ground standing biomass were collected by clipping 0.05m^2 (0.5 x 0.1m) of grass cover as close to the ground as possible from each treatment plot from all five exclosures approximately once a month (average inter-cropping period = 33 days) over the 12-month study period. Clipped samples were separated into green leaf, dry leaf, green stem, dry stem, forb leaf, and forb stem and then dried in the sun till weights reached a steady-state. Dry mass of separated categories were weighed using an electronic balance to a tenth of a gram. Over 98% of the herbaceous biomass sampled were grasses, of which the dominant species were the perennials *Bothriochloa pertusa*, *Heteropogon contortus*, *Eragrostis atropurpurea*, and *Digitaria spp*., and to lesser extent *Sporobolis indicus* and *Themeda tremula*.

Leaf nitrogen concentration in four different seasons—late wet (25 October 2006), mid dry (31 January 2007), late dry (01 March 2007) and early wet (15 June 2007)—were measured using an automated nitrogen analyzer at the National Institute of Animal Nutrition and Physiology, Bangalore, India.

Samples (n = 5) of the top 10 cm of the soil were collected prior to the experiment, and from all the control and main treatment effect plots at the end of the experiment (n = 5 for each treatment and control), to measure the following soil properties: total nitrogen content (determined using Kjeldahl analysis); organic content (determined using the Walkley-Black method); phosphorus content (determined using the Olsen and Bray methods); and pH and electric conductivity (EC%), (determined using a potentiometer; Carter & Gregorich, 2008).

Statistical analysis

Separate repeated-measures ANOVA tests were used to detect differences in 1) standing biomass between the different treatments, 2) seasonal variation of graminoid leaf nitrogen content, and 3) between grazed and untreated ungrazed plots. To satisfy the repeated measures

GLM model condition of equality of error variances, we analyzed the biomass data transformed to their natural logarithms. In the repeated-measures ANOVA analysis of standing biomass, the Mauchly's test indicated that the assumption of sphericity had been violated (χ^2 (54) = 90.79, P = 0.001). Therefore, the degrees of freedom were corrected using the Greenhouse-Geisser estimate of sphericity (ε = 0.63) and reported standing biomass statistics are Greenhouse-Geisser estimates (Table 2.1). In the repeated-measures ANOVA analysis of leaf nitrogen concentration (expressed as % DM) the Mauchly's test indicated that the assumption of sphericity was not violated (χ^2 (5) = 9.68, P = 0.09). These analyses were done using SPSS *v*.15.

Results

Herbaceous growth (estimated by the difference between two successive monthly biomass measurements of the ungrazed control plots; Appendix 2.1) occurred May – December, i.e., during the rainy season and a short period of the immediate cool winter, and not during the dry season. The highest rate of daily biomass change (calculated by dividing the difference in biomass of two successive sampling occasions by the number of days between the sampling occasions) was recorded in the month of October (0.81% day^{-1}). Ungrazed (within the exclosures) standing biomass was at its highest at the end of the rains (January) and at its lowest in the late dry season (March – April) (Appendix 2.1; Fig. 2.1). In January leaf biomass was only 40% of total biomass, and its live component only 10% (Figs. 2.2a,b), implying that the high graminoid biomass availability in January was of high fibre content as a result of increased investment by plants in structural components like stems in the latter half of the growing season. Also, herbaceous leaf biomass was highest in September and lowest in March (Fig. 2.2a).

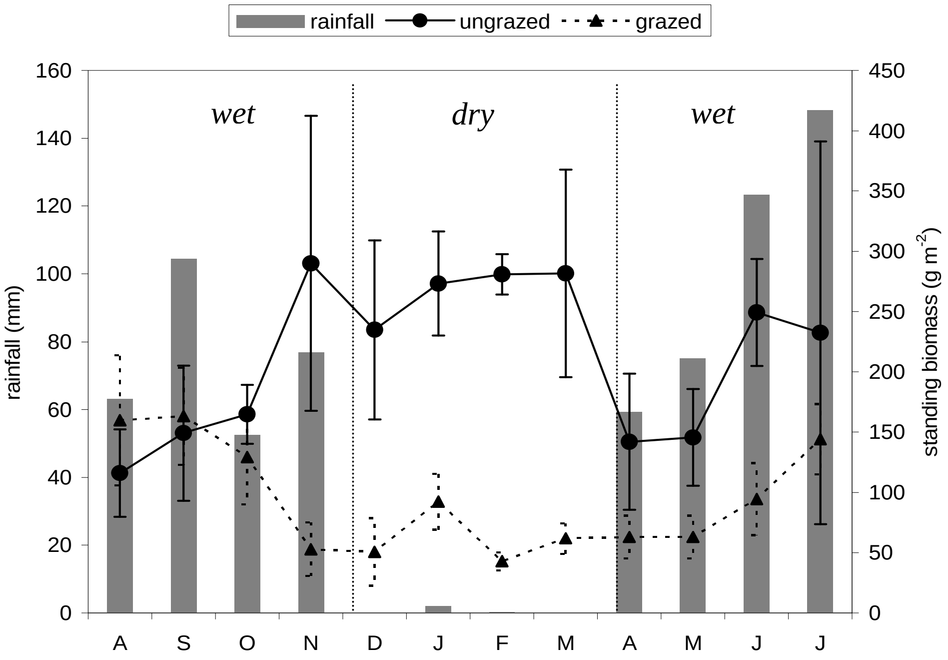


Fig. 2.1. Rainfall in Masinagudi (2 km north of experiment location) and means of standing biomass found in all treatment plots (± 95% CI) of a fully factorial 3x3 (nitrogen and water) grazing exclosure experiment in South India, August 2006-July 2007.

The range of standing crop biomass found in the control plots within the exclosures was 116 – 320 g m^{-2}. Standing crop biomass was significantly greater within the exclosure (the control ungrazed plots) than the grazed plots (F(1, 8) = 75.56, $P < 0.001$), and varied unimodally over time across all treatments (Fig 2.1). The difference in standing crop biomass between the nitrogen treatment levels was significant, but not between the water treatment levels or the nitrogen*water treatments (Table 2.1). There was a significant positive effect of nitrogen on biomass production when comparing level 0 (no addition) to both level 1 (P =0.01) and level 2 ($P < 0.001$), while the difference between levels 1 and 2 was not significant (P = 0.21). The differences between different water treatment levels in general were insignificant: between levels 0 and level 1 (P = 0.14); levels 0 and 2 (P = 0.55); and levels 1 and 2 (P = 0.40). Standing biomass was significantly greater within the exclosure (the control ungrazed plots) than outside the exclosures on highly grazed plots (F(1, 8) = 75.56, $P < 0.001$).

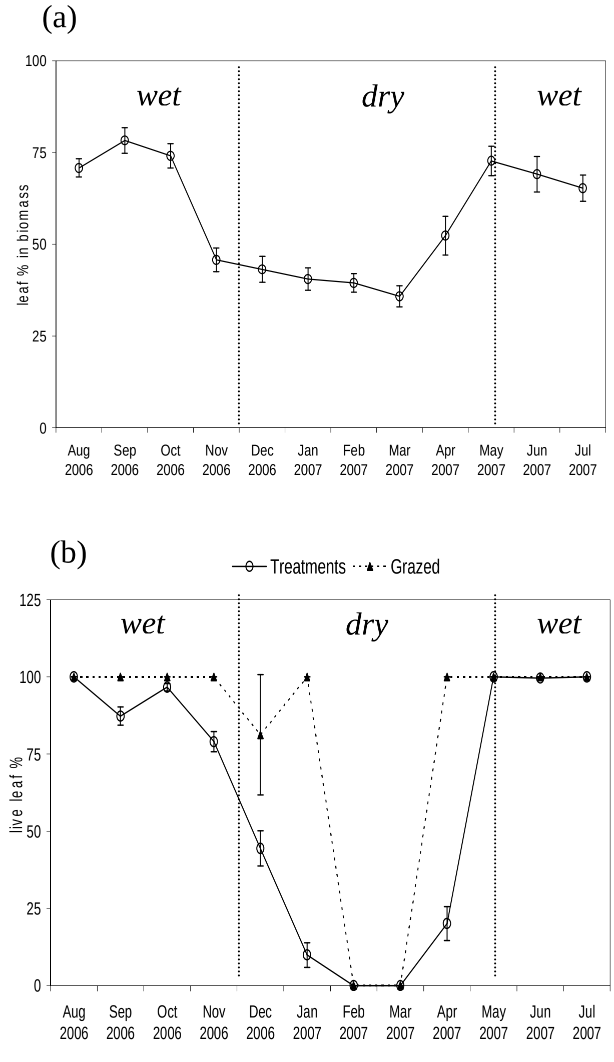


Fig. 2.2. a) Leaf, and b) live leaf % (± 95% CI) in standing biomass of the herbaceous layer found in all fertilizer and water treatment plots of a exclosure experiment in South India, July 2006-July 2007. Standing biomass inside was compared to biomass outside the exclosures in (b).

Table 2.1. Results of a repeated measures ANOVA of above ground primary production standing biomass from a fully factorial 3x3 (nitrogen and water) treatment grazing exclosure experiment in South India. Statistics reported are corrected Greenhouse-Geisser estimates of the ANOVA model. Significant values are reported in bold font.

Source	df	F	P
Intercept	1	3030.75	< **0.001**
Block	1	10.15	**0.003**
Nitrogen	2	7.87	**0.002**
Water	2	1.13	0.33
Nitrogen * Water	4	0.61	0.66
Error	34		
Time	6.30	23.17	< **0.001**
Time * Block	6.30	5.84	< **0.001**
Time * Nitrogen	12.61	1.48	0.13
Time * Water	12.61	1.61	0.09
Time * Nitrogen * Water	25.21	1.19	0.25
Error	214.29		

Table 2.2. Results of a repeated measures ANOVA of gaminoid leaf nitrogen content from a fully factorial 3x3 (nitrogen and water) treatment grazing exclosure experiment in South India. Significant values are reported in bold font.

Source	df	F	P
Intercept	1	1084.25	< **0.001**
Block	1	5.75	0.023
Nitrogen	2	9.21	**0.001**
Water	2	2.10	0.15
Nitrogen*Water	4	0.45	0.78
Error	29		
Time	3	35.20	< **0.001**
Time * Block	3	5.79	**0.001**
Time * Nitrogen	6	1.80	0.11
Time * Water	6	3.80	**0.002**
Time * Nitrogen * Water	12	2.07	**0.027**
Error	87		

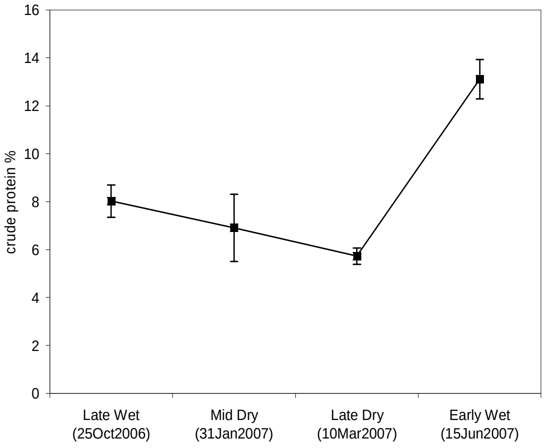


Fig. 2.3. Mean leaf nitrogen % (± 95% CI) in standing biomass found in all treatment plots of a fully factorial 3x3 (nitrogen and water) treatment grazing exclosure experiment in South India.

Leaf crude protein content (leaf nitrogen content * 6.25) varied significantly between the seasons (5.72 – 13.11%; Appendix 2.1) and was highest in the early wet season, and lowest in the late dry season (Fig. 2.3). The nitrogen, but not the water, treatments had a significant positive effect on leaf nitrogen content (Table 2.2). The positive effect of additional nitrogen was significant between plots that received 21 g N m^{-2} yr^{-1} (level 2) and those that received no nitrogen (level 0) (P = 0.002) and those that received 7 g N m^{-2} yr^{-1} (level 1) (P = 0.07); the difference between levels 0 and 1 was insignificant (P = 0.87). The response of leaf nitrogen to the water treatments was similarly insignificant between levels 0 and 1 (P = 0.84), levels 0 and 2 (P = 0.49), and levels 1 and 2 (P = 0.15) (Appendix 2.2; Table 2.2).

In the absence of grazing the live % of the leaf component in graminoid biomass was 100% for the first half of the wet season (May-August), had declined to 0% by the mid-dry season (February), and was again back at 100% with the onset of a new wet season (Fig. 2.2b). Neither nitrogen nor water addition changed the pattern in leaf production in the absence of grazing. Grazing appeared to stimulate new leaf production as the live component in leaf biomass was higher for a longer duration in the grazed plots than the ungrazed plots (Fig. 2.2b).

Using a one-way ANOVA, we found no significant difference in soil properties across the fences nor between pre-experiment and post-experiment (control and main effects) plot samples for Kjeldahl N (0.11 – 0.24%), organic carbon (0.84 – 2.15%), and pH (5.06 – 6.5), but we did find that electrical conductivity (0.04 – 0.33 mhos cm^{-1}) were higher in soils that were treated with nitrogen (0.14 ± 0.06 95% CI) in contrast to pre-experiment (0.06 ± 0.02 95% CI) and post-experiment control (0.06 ± 0.02 95% CI) and water treated (0.07 ± 0.02 95% CI) soils.

Discussion

We found aboveground graminoid production in South India to be nitrogen limited. This limitation was highlighted by the positive biomass response to the addition of even small amounts of nitrogen (7 g N m^{-2} yr^{-1}). Furthermore, the absence of a positive response in soil nitrogen levels to the nitrogen treatments indicated that the added nitrogen was rapidly absorbed by the graminoid species. It is worth noting that both the above responses—the additional biomass production and the rapid absorption of nitrogen—were both recorded despite below average annual precipitation during the study period, conditions which should have favoured herbaceous growth responding more to the water, than the nitrogen treatments.

As predicted, plant nitrogen was at its highest during the early wet season and lowest in the late dry season. Furthermore, Table 2.3 shows that while leaf nitrogen content is comparable to some areas in Africa, it is at the lower end of the global range. Therefore, large herbivores in the area live in low quality (leaf nitrogen) conditions. Since nitrogen levels were the lowest (Fig. 2.3), and fibre content were the highest (Figs. 2.2a,b), during the dry season, it is during the dry season that large herbivore species would be most challenged to satisfy their nutritional requirements. This would be particularly true for smaller species and even more so for lactating females, and prevailing conditions have the potential to influence the timing of parturition of smaller species (Rutberg, 1987).

Although the high nitrogen content available in young shoots of graminoids in the early wet season appear to be ideal forage for large herbivores, this might be the case only for smaller species. A sudden change from a low to a high quality diet has the potential to cause acidosis, a condition that lowers the digestive capabilities of the rumen (Van de Veen, 1979; Van Soest 1994). Therefore, for large roughage forager species like gaur—species that have a large bite size and for whom high quality forage is less of a necessity—the high quality short fresh flush in the early wet season (April-May) is less attractive than it is for smaller species. Their greater need for high quality forage and their smaller bite size, means that smaller species would strive to maximize their intake of high quality herbaceous forage during the early wet season.

Table 2.3. Leaf nitrogen content of grass species/herbaceous layer in tropical ecosystems around the world.

Location	Leaf nitrogen (%)	Source
Global review	1-6	Mattson, 1980
Floodplain grassland, Amazon (3°15’ S, 60°00’ W)	1.5-2.5	Piedade *et al.*, 1992
Themeda triandra (Africa)	1.0-1.6	Coughernour *et al.*, 1985
Indigofera spinosa (African shrub)	2.3-2.8	Coughenour *et al*., 1985
Water treated grasslands, Amboseli, Kenya (2° 30' S; 37° 15' E)	2.6-4.1	Georgiadis *et al*., 1989
Lake Manyara National Park, Tanzania (3°30’ S, 35°45’ E)	0.8-3.8	Prins & Beekman, 1989
Tarangire National Park, Tanzania (3°35’ S, 35°55’ E)	3.5 (early wet)	Voeten & Prins, 1999
Mkwaja North, Tanzania (5°43’ S, 38°47’ E)	0.4-2.4	Treydte *et al*., 2006
Greater Kruger Park, South Africa (24°17-78' S, 30°66'-31°26' E	0.6-1.9	Treydte *et al*., 2008
Boucle du Baoule, Mali (13°45’ N, 9°20’ E)	0.76-4.5	de Bie, 1991
North American grasslands	1.6-1.8	Milchunas *et al*., 1995
Masinagudi, India South India (11°55’ N, 76°63’ E)	0.7-2.3	This study

We also found evidence to support our prediction that additional moisture in the dry season would not affect graminoid production, neither by increasing biomass production nor by extending the growing season (measured by live % of leaf biomass; Fig. 2.2b). This suggests high water-use efficiency by the herbaceous layer, which is consistent with the fact that all dominant grass species recorded in our experiment plots were C_4 species; high water-use efficiency is common to majority of C_4 plant species (Hsiao & Acevedo, 1974; Bacon, 2004). This physiological advantage enables plants living in areas that experience temporally variable (seasonal as well as annual) moisture—the study site receives all its annual rainfall via a variable monsoon rainfall for its moisture—to absorb adequate moisture required for their growth. In the Sahel the high water-use efficiencies by herbaceous plants have been identified as the reason why the growing season ends before the depletion of the ground water in the dry season despite prevailing conditions of low rainfall and high evaporation (Breman & De Wit, 1983).

Table 2.4. Above-ground biomass estimates of herbaceous layer in tropical ecosystems around the world, in the presence and absence of grazing.

Location	Highest above-ground biomass (g m^{-2})	Rainfall (mm y^{-1})	Source
Nairobi National Park, Kenya (1°’ N, 36° E)	338	950	Kinyamario & Macharia, 1992
Nairobi National Park, Kenya (1°20’ N, 36°50’ E)	332	850	Deshmukh, 1986
Kaputei plains, Kenya (1°30’ N, 36°40’ E)	309	900	Owaga, 1980
Guinea savannas, Nigeria (9°18’ N, 5°04’ E)	435	1175	Ohiagu & Wood, 1979
Lamto savannas, Ivory Coast (5°02’ N, 6°13’ E)	420	1300	Menaut & Cesar, 1979
Boucle du Baoule, Mali (13°45’ N, 9°20’ E)	300	900	de Bie, 1991
Pilbara,Northwest Australia (22°17’ N, 117°40’ E)	≅500	350	Bennett & Adams, 2001
Ban Klong Hoi Khong, Thailand (6° N, 100 ° E)	347	2100	Kamnalrut & Evenson, 1992
Vindhyan Plateau, Central India (24°18’ N, 82°59’ E)	741	1035	Pandey & Singh, 1992
Kurukshetra, North India (29°58’ N, 76°51’ E)	1740	800	Singh & Yadava, 1974
Rudranath, North India (30°28’ N, 79°20’ E)	918	1600	Ram *et al*., 1989
Bandipur, South India (11°47’ N, 76°23’ E)	300	1100	Devidas & Puyravaud, 1995
Masinagudi, South India (11°55’ N, 76°63’ E)	320	860	This study

The standing biomass estimates within the exclosures were comparable to biomass levels found within exclosures in savannas and other tropical habitats of Africa and Asia (Table 2.4). This similarity in productivity levels offers one explanation as to why South India manages to support populations of large herbivore assemblages that include megaherbivore grazers like elephant and gaur. Biomass estimates from the study site were lower, however, when compared to other sites in North India (Table 2.3). Table 2.3 shows that annual rainfall is similar in both regions (except for the much higher 1600 mm that Rudranath receives). North India has richer soil nutrients as a function of constant replenishment by alluvial deposits from multiple rivers originating in the Himalayas, and Central Indian soils are considered to be rich as a function of the volcanic activity of the Deccan Traps. This offers one explanation as to why graminoid biomass estimates in Northern India is higher than biomass estimates in the South. Soil nitrogen levels found at the study site were, however, similar to levels found in other tropical areas that support large herbivore assemblages (Table 2.4).

Although light to moderate grazing has been shown to increase primary production by 45% in Central India (Pandey & Singh, 1992), the high grazing intensity on our grazed plots probably reduced biomass production similar to what has been found in other sites (Milchunas & Lauenroth, 1993). Grazing, though, appeared to extend the growth period of the herbaceous layer in the study area—green leaf % remained higher and for a longer period in the grazed plots (Fig. 2.2b)—which is similar to what has been found in North Indian and African savannas (McNaughton, 1984; Milchunas *et al*., 1995; Augustine & McNaughton, 2006).

In conclusion, this study provides evidence that herbaceous biomass production in South India is limited by nitrogen availability and is not affected by additional moisture despite a below average rainfall year. We found evidence that grazing can lengthen the growing period of graminoids in the area. Graminoid biomass levels were similar, but nutrient (nitrogen) levels were low, when compared to other tropical areas. The low nitrogen and high fibre levels in the dry season have the potential to impact the ecology and biology of smaller herbivore species in South India.

Appendix 2.1. Means ± 95% CI (g m^{-2}) of dry matter above ground standing biomass harvested every month from a full factorial 3x3 (nitrogen and water) treatment grazing exclosure experiment in South India. Treatments: N Level 1 = addition of 7g N m^{-2} yr^{-1}; N Level 2 = addition of 12g N m^{-2} yr^{-1}; Water Level 1 = addition of 300mm/m^2 spread over the wet season; Water Level 2 = addition of 300mm/m^2 spread over the entire year. N treatments added in the form of NH_4NO_3.

Date Treatment	Jun. 2006 *(Pre-Exp.)*	Aug. 2006	Sep. 2006	Oct. 2006	Nov. 2006	Dec. 2006	Jan. 2007	Feb. 2007	Mar. 2007	Apr. 2007	May. 2007	Jun. 2007	Jul. 2007
Control	125.2 ± 25.6	116.0 ± 36.1	149.2 ± 56.0	164.8 ± 24.4	290.0 ± 122.3	234.8 ± 74.2	273.2 ± 43.2	280.8 ± 16.7	281.6 ± 86.0	142.0 ± 56.4	145.6 ± 40.2	249.2 ± 44.4	232.4 ± 158.9
N Level 1	103.6 ± 24.7	147.6 ± 74.5	151.2 ± 53.0	178.4 ± 55.7	264.0 ± 125.9	261.2 ± 31.6	326.8 ± 57.3	270.4 ± 75.3	402.0 ± 136.8	221.2 ± 56.3	120.4 ± 47.0	266.0 ± 61.6	201.2 ± 42.8
N Level 1 + Water Level 1	116.0 ± 20.4	113.2 ± 25.4	156.0 ± 28.3	236.8 ± 60.9	317.6 ± 116.9	367.6 ± 75.6	301.6 ± 16.5	304.0 ± 89.4	304.0 ± 89.4	218.0 ± 71.0	153.2 ± 45.9	249.2 ± 44.4	223.2 ± 61.1
N Level 1 + Water Level 2	110.8 ± 37.4	138.8 ± 19.0	154.0 ± 54.3	227.2 ± 64.0	296.0 ± 75.3	304.8 ± 33.4	372.8 ± 106.7	298.8 ± 30.1	319.2 ± 66.0	210.8 ± 57.8	160.8 ± 55.2	194.8 ± 37.4	254.8 ± 67.0
N Level 2	87.2 ± 18.4	141.2 ± 37.7	153.2 ± 31.0	237.2 ± 99.7	330.8 ± 94.4	290.8 ± 55.1	407.2 ± 104.5	285.2 ± 33.0	216.0 ± 9.2	258.4 ± 83.9	144.4 ± 24.8	221.6 ± 40.7	199.6 ± 51.4
N Level 2 + Water Level 1	110.8 ± 35.3	143.2 ± 34.4	192.4 ± 64.8	228.8 ± 47.4	353.6 ± 146.2	417.6 ± 131.9	374.0 ± 94.1	356.0 ± 106.6	404.4 ± 145.9	185.2 ± 65.4	134.0 ± 36.3	195.6 ± 28.9	330.4 ± 105.3
N Level 2 + Water Level 2	88.8 ± 17.0	177.6 ± 76.6	152.4 ± 53.5	255.6 ± 54.2	255.6 ± 31.6	426.8 ± 112.0	386.4 ± 98.6	319.2 ± 74.9	291.2 ± 63.1	174.0 ± 91.2	164.8 ± 44.0	197.2 ± 39.3	208.0 ± 58.9
Water Level 1	86.8 ± 8.6	103.6 ± 42.5	126.0 ± 15.2	195.2 ± 48.8	272.0 ± 81.1	289.2 ± 72.4	287.6 ± 49.4	284.4 ± 36.3	314.4 ± 66.7	166.4 ± 85.0	141.2 ± 51.7	186.4 ± 34.1	198.8 ± 47.7
Water Level 2	90.4 ± 24.4	67.6 ± 29.2	104.8 ± 37.3	*Lack of data*	293.6 ± 121.5	358.0 ± 53.3	278.0 ± 17.5	263.6 ± 30.6	246.8 ± 29.6	196.0 ± 108.9	139.6 ± 31.0	210.0 ± 42.6	247.6 ± 57.4
Grazed	92.4 ± 31.1	56.8 ± 19.2	58.0 ± 14.2	46.0 ± 14.0	18.8 ± 7.9	18.0 ± 10.0	32.8 ± 8.2	15.2 ± 2.7	22.0 ± 4.5	22.4 ± 6.2	22.4 ± 6.2	33.6 ± 10.7	51.2 ± 10.4

Appendix 2.2. Means ± 95% CI (g m^{-2}) of leaf nitrogen content in ground standing biomass harvested from a fully factorial 3x3 (nitrogen and water) treatment grazing exclosure experiment in South India.

	Late Wet 25Oct 2006	Mid Dry 31Jan 2007	Late Dry 10Mar 2007	Early Wet 15Jun 2007
Control	8.02 ± 0.68	6.91 ± 1.40	5.72 ± 2.56	13.11 ± 0.82
Level 1	9.74 ± 1.33	7.36 ± 0.59	6.48 ± 1.02	10.94 ± 2.22
N Level 1 + Water Level 1	7.85 ± 0.98	7.97 ± 1.20	6.78 ± 2.71	11.46 ± 0.79
N Level 1 + Water Level 2	8.82 ± 3.51	7.57 ± 1.04	5.64 ± 0.69	10.53 ± 0.78
N Level 2	10.81 ± 1.19	8.20 ± 0.99	6.35 ± 0.86	11.65 ± 0.86
N Level 2 + Water Level 1	10.62 ± 1.44	8.39 ± 1.64	7.55 ± 1.14	11.91 ± 1.28
N Level 2 + Water Level 2	9.96 ± 1.52	9.51 ± 0.70	7.21 ± 1.18	10.75 ± 1.01
Water Level 1	9.10 ± 3.72	8.11 ± 1.84	6.44 ± 1.55	10.43 ± 0.87
Water Level 2	7.53 ± 3.03	7.61 ± 1.00	5.44 ± 2.30	9.47 ± 0.87

3

The role of body mass in diet and habitat selection by large herbivores species in a tropical South Indian forest

Farshid S. Ahrestani, Ignas M.A. Heitkönig and Herbert H.T. Prins

Abstract

Body mass, digestive physiology, and forage availability play key roles in determining diet and habitat selection by large herbivore species. With the goal to better understand diet and habitat selection of herbivore species in South India, we tested hypotheses predicting differences in the diet and habitat selection made by species of varying body mass and digestive strategies. For a year we studied the seasonal differences in diet and habitat selection of three ruminant species of varying body mass (gaur *Bos gaurus*, sambar *Cervus unicolor*, and chital *Axis axis*) and the large hindgut fermenter elephant *Elephas maximus* in South India. We also determined seasonal variation in grass quality, used $\partial^{13}C$ analysis of faecal samples, and conducted a grid based survey to determine the grass:browse in species diets, their habitat selection, and their niche breadth and its overlap with that of the other species. We found chital increased the proportion of non-graminoids in their diet as the wet season changed to the dry; gaur showed preference for grasses throughout the year; sambar showed preference for browse throughout the year; and elephants were found to be mixed feeders. Gaur niche breadth in the study area was the smallest, and although equally small in both seasons, gaur clearly preferred the wetter moist deciduous region in the dry season and dry deciduous habitat in the wet season. Elephants niche breadth was high and had a high equal overlap with that of the other species in both seasons. Sambar utilized the study area extensively and their ‘niche breadth’ was high in both seasons, suggesting that sambar are capable of supporting their metabolic requirements from different habitats. In general, our results showed that it is possible to predict seasonal diet selection by small ruminant (chital) and large hindgut (elephant) species, but not that of intermediate ruminants (sambar and gaur) based on body mass based principles.

Introduction

Body mass plays an integral role in the diet and habitat selection by large mammalian herbivores (Bell, 1970; Jarman, 1973; Illius & Gordon, 1987; Wilmshurst *et al.*, 2000). The core principle that explains the effect of body mass on large herbivore foraging ecology is Kleiber's (1932) ¾ power function of a species' metabolic requirements (West *et al.*, 2002; Brown *et al.*, 2004). Coupling Kleiber's ¾ power function—which explains that with increasing body mass animals require less energy per unit body mass—and the linear allometric function of gut volume of large herbivores (particularly ruminants), tells us that larger herbivore species are better equipped to satisfy their metabolic requirements on low quality forage than smaller species (Demment & Van Soest, 1985; Illius & Gordon, 1992; Van Soest, 1994). This advantage that larger herbivores have over smaller herbivores is assumed to be the main mechanism that facilitates resource partitioning among species of different body mass, and is commonly called the Jarman-Bell principle (Geist, 1974).

Although larger herbivores have an advantage over smaller species with respect to subsisting on low forage quality, they also have, though, higher metabolic requirements per unit time than smaller species (Moen, 1973). It logically follows, then, that larger species—in order to find resources to satisfy their larger metabolic requirements—probably need larger areas than smaller species. This hypothesis is supported by the positive relationship that has been observed between species body mass and their home range area (McNab, 1963; Damuth, 1981; Lindstedt *et al.*, 1986; Jetz *et al.*, 2004).

The impact of a species' digestive physiology complements the impact that body mass has on a species' foraging ecology. Large herbivores either have foregut (ruminant) or hindgut fermentation digestive physiologies. The major difference between these systems is that hindgut fermenters have faster passage rates and thus shorter retention times (Van Soest, 1994; Clauss *et al.*, 2003). This, therefore, enables hindgut fermenters to survive on low forage quality levels similar to those that only relatively larger ruminants can tolerate (Demment & Van Soest, 1985; Clauss *et al.*, 2003).

In addition to the impact of intrinsic factors like body mass and digestive strategy, it is obvious that extrinsic parameters such as the spatial and temporal variation in plant quality, also obviously affect herbivore foraging ecology. For example, in tropical areas with wet-dry cyclic weather patterns, plant quality varies seasonally (Prins & Loth 1988; Beever *et al.*, 2000). During the early wet season, when green grass is of low fibre and high nutrients, it is easier for herbivores to find high quality forage. As the wet progresses to the dry season, grasses invest more in structural carbohydrates (fibre). In the dry season, therefore, grass carbon:nitrogen ratios are at their highest and quality levels at their lowest. As such, in areas where the year is divided into wet and dry seasons, it is in the dry season that large herbivores are most challenged to satisfy their metabolic requirements.

The majority of empirical studies that have helped better understand the impact of the above intrinsic and extrinsic parameters on large herbivore foraging ecology in the tropics have emerged from Africa. A major reason for this is because Africa offers the opportunity to study the world's richest (≅ 30 species) large herbivore communities, often with the added advantage of multiple species of the same genera. In spite of its lower species richness levels (alpha species richness = 10 maximum), the 10 – 3100 kg body mass range of India's large herbivore assemblage is as wide as Africa's 10 – 4500 kg body size range. While there is no overlap of species between the large herbivore assemblages in India and Africa, both include megaherbivores like elephant and rhino, which explains their similarly wide body size ranges. Similar to Africa, India's assemblage also has a mix of both hindgut and foregut fermenter species. Therefore, since all the necessary conditions are met—a wide body mass range and a mix of hindgut and foregut fermenter species—India's herbivore assemblage presents a suitable case study for testing whether body mass based principles (for e.g. the Jarman-Bell principle) can help predict large herbivore foraging ecology.

We chose to study, therefore, an assemblage of four large herbivore species—three ruminants species (the 60 kg chital *Axis axis*, 200 kg sambar *Cervus unicolor*, and 700 kg gaur *Bos gaurus*) and a large hindgut fermenter (3100 kg Asian elephant *Elephas maximus*)—in a South Indian tropical forest with seasonally variable forage quality, with the goal of testing the following predictions of diet and habitat selection by different body mass species:

1) Because of their higher forage quality requirements the smallest of the three ruminant species, chital, would be affected the most by decreasing grass quality as the wet season changed to the dry. We predicted therefore that chital would decrease the proportion of grasses in their diet earlier, and to a higher proportion, than the larger ruminants sambar and gaur.

2) Elephants have large metabolic requirements and because they are mega-hindgut fermenters they also have low digestive efficiencies and retention times. In general, therefore, elephants are less selective bulk mixed feeders that require a large area to satisfy their metabolic requirements (Sukumar 1990, 1992). We, therefore, predicted that elephant diet and 'niche breadth' would be highest among the species and would overlap equally and to a high degree with the diet and 'niche breadths' of the other three ruminant species.

Methods

Study area

The study area (11^{o}32$^{'}$-41$^{'}$N, 76^{o}22$^{'}$-41$^{'}$E) was spread over two contiguous Tiger Reserves in South India, Mudumalai and Bandipur (Fig. 1.1) and measured 400 km^{2}. This area is located on the lower elevations of the Western Ghats and has undulating terrain 250 - 400m. The rainfall in monsoon driven and its annual average is 1050mm. There are three primary seasons: a Southwest monsoon wet (May-July: 60% of rainfall), a Northeast monsoon wet (August-November: 40% of rainfall) and a dry (December-March) (Table 3.2.).

The study area has a dry east – wet west moisture gradient which has resulted in the east being dominated by dry deciduous forests and the west by moist deciduous forests (the extreme east is thorn-scrub and the extreme west is semi-evergreen). The study area's understory (particularly in the dry deciduous region; Table 3.2) is dominated by non-native invasive species—primarily *Lantana camara* and *Chromolaena odorata*, and to a lesser extent *Parthenium hysterophorus*—that not only have displaced palatable grasses but are also not preferred forage for large herbivores.

Field data

Herbaceous layer quality measurements

To measure forage quality, the aboveground herbaceous layer was sampled in the dry deciduous region at monthly intervals. Ten to thirty samples were collected per month by clipping quadrants 0.5 m x 0.5 m in size. Clipped samples were separated into live and dead leaves and stems, sun-dried till constant mass and weighed. Nitrogen content of 2 – 4 randomly selected monthly samples of green leaves were measured using an automatic nitrogen analyzer at the National Institute of Animal Nutrition and Physiology, Bangalore, India.

Faecal sampling

As it was difficult to observe species foraging in the field, we collected and analyzed faeces to measure diet composition. Faecal samples of all four species were collected every month from May 2006 to July 2007 from the dry deciduous region. At least 90 % of the samples were collected in the middle of each month from distinct faecal piles which were always moist

(< 1 - 2 days old) to ensure they represented monthly samples appropriately.

Grid-based sampling

To measure 'niche breadth and overlap' and habitat selection, the study area was sampled using a grid-based survey. The area was divided into *n* = 250 1 km x 1 km square grid cells, and alternate grid cells (*n* = 123) were sampled using a 0.5 km x 2m strip transect along their diagonals. Faecal piles of the four species were counted along the length of a transect, and habitat parameters within each grid cell were measured using five circular plots of 5m radius along the transect at 100m intervals. We used the mean from the five point samples from each grid cell as the measure of a grid cell habitat parameter (Table 3.1).

Table 3.1. List of habitat variables measured in circular plots of 5m radius along strip sampling transects during a grid-based survey of the study area. Grass height was estimated to the closest 5cm multiple. The cover percentage variables were quantified categorically: 0 = absent; 1 = 1-25%; 2 = 26-50%; 3 = 51-75%; 4 = 76-100%.

Habitat parameters	Unit	
Grass height	cm	
Grass cover	%	
Tall-grass cover	%	
Lantana spp. cover	%	
Chromolaena sp. cover	%	
Tree numbers: counted in categories	dbh = 0-2cm	S
	dbh = 20-80cm	M
	dbh > 80cm	T

Laboratory analysis

Monthly faecal composite samples were made by pooling at least five randomly selected faecal samples (except for January and February 2007 when the sample size was three) for each species. Subsamples of these monthly composite samples were chemically analyzed to measure diet composition of the four herbivore species using carbon isotope analysis. Undigested forage in faeces have been shown to consistently and accurately reflect the isotopic composition of the forage ingested by a herbivore (Vogel, 1978; Tieszen *et al.*, 1979). A measure of stable carbon isotope ratio ∂^{13}C (^{13}C/^{12}C) of the faeces provides a reliable proxy of the relative proportion of C_3 (grasses and browse) to C_4 (grasses and sedges) species consumed by a species (Cerling & Harris, 1999; Sponheimer, 2003; Cordon *et al.*, 2007). Since the majority of grass species in the study area were C_4 species and the browse species were primarily C_3 species, meant that the stable isotope ratio measured the grass:browse ratio of the diet. As we were analyzing composite samples we chose to analyze only two subsamples from each composite and report their mean. The spectrometry analysis of the faeces were done at the Isotope Laboratory, Agricultural University, Bangalore, India.

Statistical analysis

Using a kernel-based GIS solution (Hawthe Tools) we mapped the extent and variation in occupancy of the four herbivore species (based on faecal-pile counts) in the study area. We also quantified the 'niche breadth' of each species using Hulbert's (1978) standardization (B_A) of Levins (1968) measure (B)

$$B_A = \frac{B-1}{n-1} \qquad \text{where} \qquad B = \frac{1}{\sum P_j^2} \qquad (1)$$

P_j^2 = proportion of individuals (based on faecal-pile counts) found in a grid cell j; n = total number of available grid cells. This estimate of ‘niche breadth’, while not disclosing much about the constituents of the ‘niche’, allows us to compare the relative use of the available habitat by the different species. In addition, we also calculated the overlap between pairs of species in both seasons using Pianka’s (1973) symmetrical measure of ‘niche overlap’ O_{jk}

$$O_{jk} = \frac{\sum^{n} p_{ji} p_{ki}}{\sqrt{\sum p_{ji} \sum p_{ki}}} \qquad (2)$$

P_{xi}= frequency of utilization grid cell i by species x. The number of dung piles found of a species in each sampled grid cell represented the proportion for eqn. (1), and frequency for eqn. (2), of each species in a grid cell.

Results

Forage quality

Analysis of herbaceous quality showed that leaf nitrogen content (1 – 2.8%; 6.5 – 18.2% crude protein) was highest in the wet season, decreased as the wet season progressed, and were at their lowest levels in the dry season (Fig. 3.1a). The percentage of leaf biomass in standing biomass (50 – 100%) and that of its green component percentage (0 – 100%) (Fig. 3.1b) were high in the wet season and low in the dry season, similar to the seasonal variation of leaf nitrogen content.

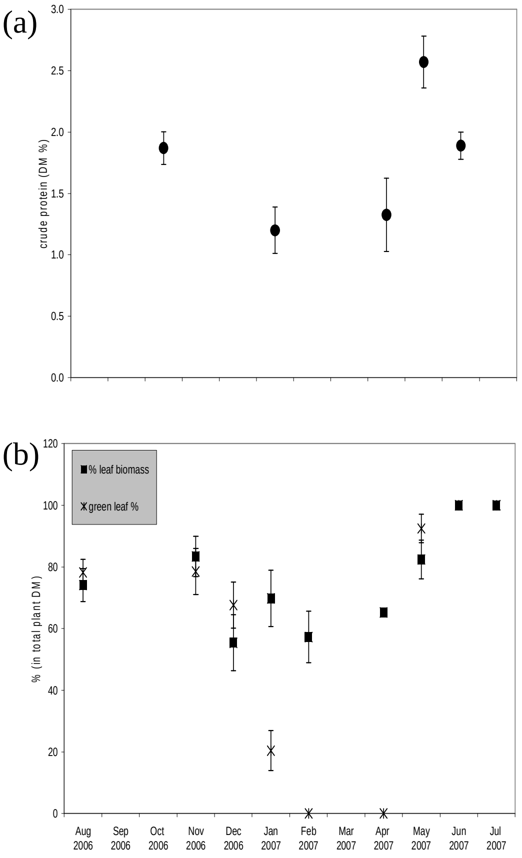
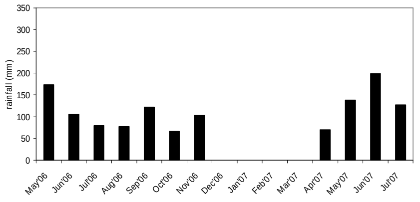
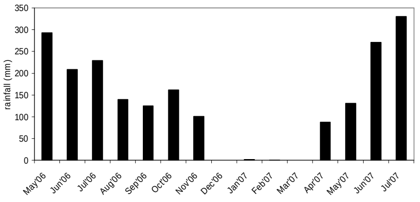


Fig. 3.1. (a) Leaf nitrogen content (mean ± 95% CI), and (b) leaf % of standing biomass (mean ± 95% CI) and its green component (mean ± 95% CI), found in herbaceous layer in dry deciduous habitat within Bandipur National Park, South India, June2006–July 2007.

Habitat comparison

Table 3.2 shows that the moist deciduous region received 800mm more rainfall than the dry deciduous region during the study period. Also, the moist deciduous region had perennial flowing streams during the dry season, while the dry deciduous region did not. These suggest that during the dry season, the probability of finding green grass would be higher in the moist than the dry deciduous region. Although *Chromolaena* was found equally in both habitats, *Lantana* was found to be three times more abundant in the dry than the moist deciduous region (Table 3.2). Tall grass habitat was taller and more abundant in the moist than the dry deciduous region, but small grass height and availability were similar in the two regions (Table 3.2). No significant correlations were found, however, between species distribution and the habitat parameters during either season.

Table 3.2. Environmental differences between the two major habitat types in study area.

		Dry deciduous forest	Moist deciduous forest
Rainfall			
(May 2006-July 2007)		(1258 mm)	(2078 mm)
*Lantana**		1.9 ± 0.3	0.6 ± 0.2
*Chromolaena**		0.7 ± 0.1	0.7 ± 0.1
Tall grass habitat*		0.5 ± 0.2	0.8 ± 0.3
Tall grass height (cm)		21.4 ± 9.1	43.5 ± 12.5
Short grass cover*		1.5 ± 0.2	1.5 ± 0.2
Short grass height (cm)	*(dry season)*	13.5 ± 1.6	11.4 ± 1.3
	(wet season)	20.1 ± 1.6	21.3 ± 1.3
Trees numbers		S (2.4 ± 0.8) M (2.4 ± 0.4) T (3.1 ± 0.4)	S (1.7 ± 0.6) M (2.5 ± 0.6) T (3.4 ± 0.3)
Water resources		Stagnant in dry season	Multiple perennial flowing streams

Habitat variables (mean ± 95% CI) found within each sampled grid cell.
* Cover % within each sampled grid cell (0-4): 0 = absent; 1 = 1-25%; 2 = 26-50%; 3 = 51-75%; 4 = 76-100%.

Grass–browse dietary composition

The low ∂^{13}C carbon isotopic ratios found for sambar suggests that sambar consumed the greatest proportion of browse among all the species throughout the year, while the elevated ∂^{13}C carbon isotopic ratios found for gaur showed that that gaur consumed the highest proportion of grasses among the four species for most of the year (Fig. 3.2). Consumption of grasses by chital was the highest in the early wet season and lowest in the mid dry season. The proportion of grasses in elephant diet was relatively high over the entire year, but a little less than the proportion of grasses in gaur diet (Fig. 3.2).

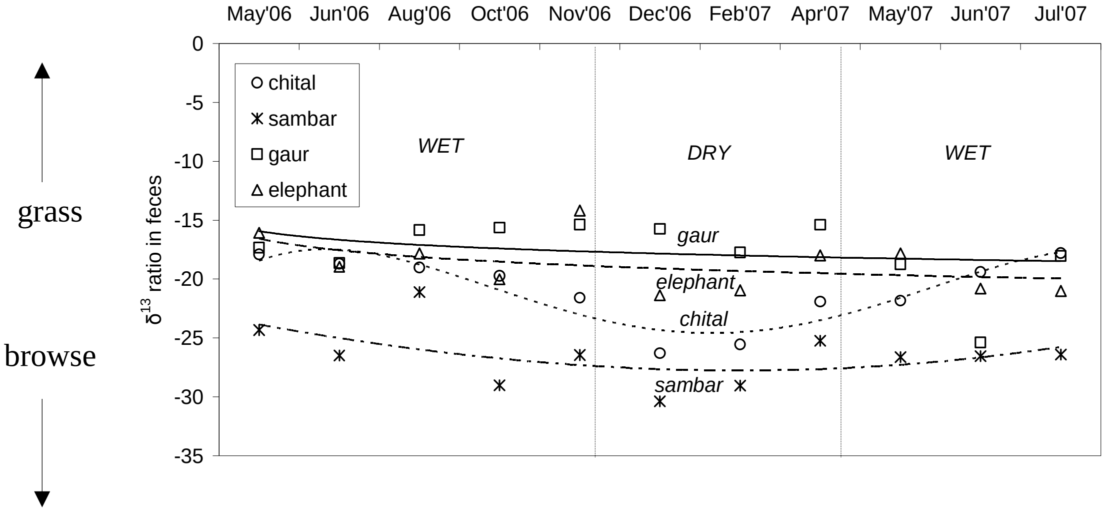


Fig. 3.2. ∂^{13}C ratio found in feces of the four largest herbivores in Bandipur and Mudumalai National Parks, South India (May 2006 – July 2007). A low ratio suggests a browse-based diet and a high ratio suggests a grass-based diet.

Niche breadth and overlap

With respect to the entire study area, all species had smaller niche breadths in the wet season; gaur niche breadth was the smallest in both seasons followed by chital, sambar, and elephant (Table 3.3). Species' niche breadth in the dry deciduous forest did not vary much between seasons, marginally decreasing for chital and sambar and increasing for elephant and gaur (Table 3.3). In the moist deciduous forest, the niche breadth of all species was higher in the wet than in the dry season: four times higher for gaur, nearly twice as higher for chital, and marginally higher for sambar and elephant (Table 3.3).

Table 3.3 shows that there is little seasonal difference in gaur niche breadth with respect to the entire study area and the dry deciduous region, but gaur niche breadth in the moist deciduous showed a four fold decrease from the dry to wet season. In addition Figs. 3.3e-f highlight an equally important point, which is that gaur occupied the wetter moist deciduous and western dry deciduous regions in the dry season and then shifted to occupying the dry deciduous region almost exclusively in the wet season. Similar to gaur, elephants too were absent in the eastern part of the dry deciduous forest, the driest region of the study area, in the dry season, but were present in this region in the wet season. This similarity in the study area seasonal occupation patterns by gaur and elephant (Figs. 3.3e-h) resulted in a high niche breadth overlap between the two species in both seasons, including a near complete overlap in the moist deciduous region in the wet season (Table 3.4).

In addition to the high overlap of elephant with gaur, the overlap of elephants with both chital and sambar in both seasons was high (Table 3.4). The niche breadth of sambar remained relatively unchanged across both seasons in both habitats (Table 3.2; Figs. 3.3c-d). Considering the entire study area, sambar niche breadth overlapped with that of chital the most, gaur the least, and was relatively high and unchanged with elephant in both seasons (Table 3.3). Chital were found to avoid the extreme western evergreen region of the study area in both seasons, the only species to do so (Figs. 3.3a,b).

Table 3.3. Nice breadth of four large herbivore species in the dry and wet seasons in Bandipur and Mudumalai Tiger Reserves, South India (2006-2007). The values presented were calculated using Hulbert's (1978) standardization (B_A) of Levins (1968) niche breadth index. Niche breadth range = 0-1, higher values indicating larger niche breadth.

Species		Wt. (kg)	Entire Study area		Dry Deciduous		Moist Deciduous	
			Dry season	Wet season	Dry season	Wet season	Dry season	Wet Season
chital	*Axis axis*	60	0.40	0.31	0.38	0.35	**0.54**	**0.29**
Sambar	*Cervus unicolor*	200	0.50	0.46	0.40	0.39	0.68	0.60
Gaur	*Bos gaurus*	700	**0.28**	0.25	0.29	0.34	**0.47**	**0.11**
elephant	*Elephas maximus*	4000	0.54	0.53	0.49	0.52	0.67	0.58

Table 3.4. Overlap in range within the study area between different pairs of four large herbivores species in the dry and wet seasons in Bandipur and Mudumalai Tiger Reserves, South India (2006-2007). Overlap between species was calculated using Pianka's (1973) symmetrical measure of niche overlap. Overlap of 1.0 indicates complete overlap and overlap of 0 indicates no overlap.

Species	Entire Study area		Dry Deciduous		Moist Deciduous	
	Dry season	Wet season	Dry season	Wet season	Dry season	Wet season
gaur.elephant	0.55	0.48	0.53	0.48	**0.94**	0.55
gaur.sambar	0.38	0.35	0.29	0.39	0.51	0.29
gaur.chital	0.26	0.38	**0.22**	**0.52**	0.57	0.53
chital.sambar	0.78	0.51	0.75	0.50	0.55	0.25
chital.elephant	0.39	0.45	0.36	0.42	0.62	0.61
sambar.elephant	0.47	0.49	0.36	0.43	0.63	0.62

In addition to the high overlap of elephant with gaur, the overlap of elephants with both chital and sambar in both seasons was high (Table 3.4). The niche breadth of sambar remained relatively unchanged across both seasons in both habitats (Table 3.2; Figs. 3.3c-d). Considering the entire study area, sambar niche breadth overlapped with that of chital the most, gaur the least, and was relatively high and unchanged with elephant in both seasons (Table 3.3.). Chital were found to avoid the extreme western evergreen region of the study area in both seasons, the only species to do so (Figs. 3.3a,b).

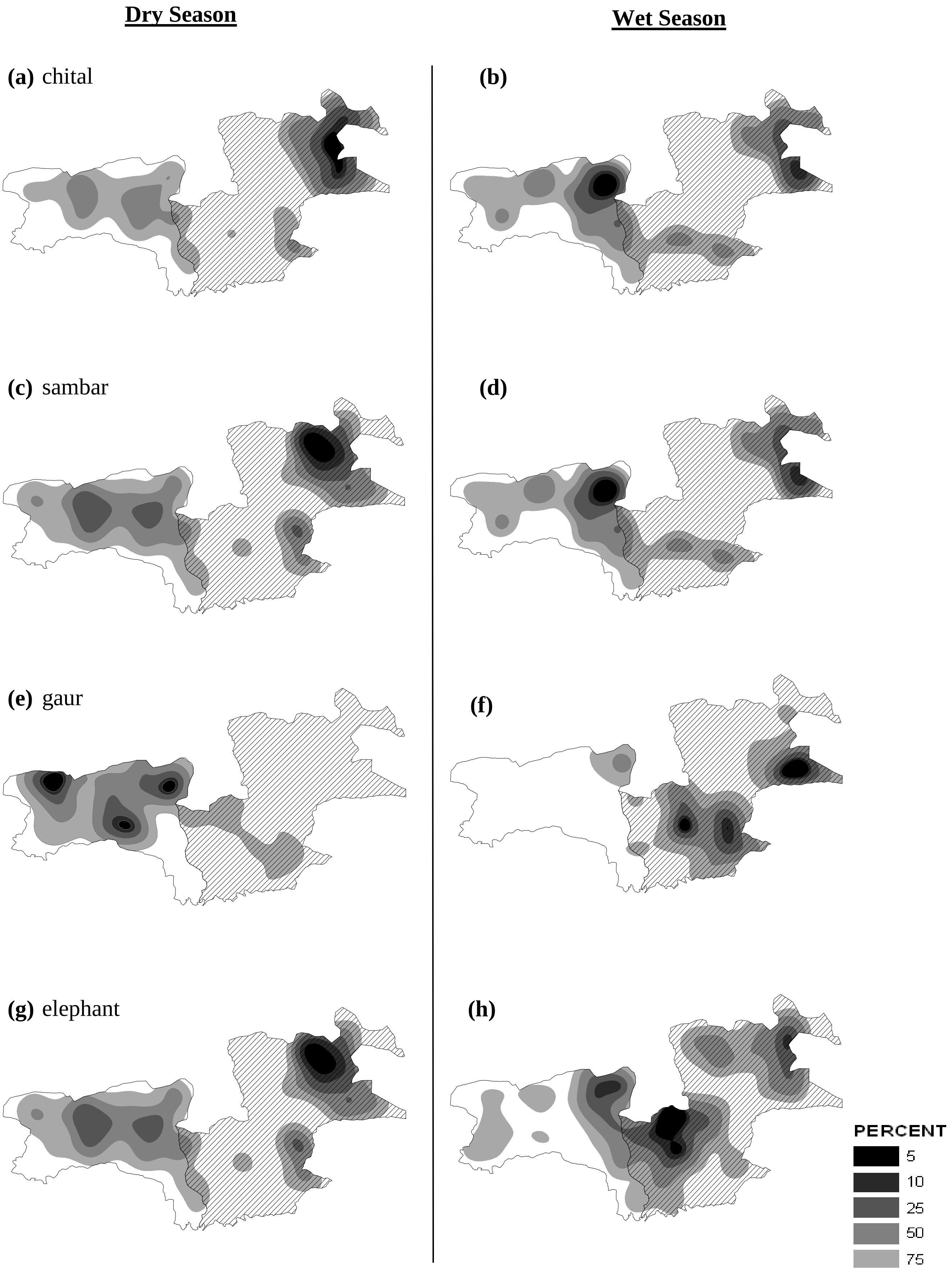


Fig. 3.3. Distribution of chital (a,b), sambar (c,d), gaur (e,f) and elephant (g,h) in the dry and wet seasons in a 400 km^2 study area in Bandipur and Mudumalai Tiger Reserves, South India, based on a grid-based survey. Percent scale: The lower the value the higher the density of species.

Discussion

The results lent support for the first hypothesis that predicted chital, and not sambar or gaur, would decrease the proportion of grasses in their diets as the wet season changed to the dry (Fig. 3.2). Other studies too have found chital to show seasonal diet preferences: In the Sub-Himalayan terai region, chital increase their consumption of grasses in recently burnt habitats during the late dry/early wet season (Mishra, 1982; Moe & Wegge, 1994, 1997). Chital were also absent from the evergreen forests in the study area, the wettest habitat (extreme western region). This finding is consistent with the fact that over its geographic range chital avoid habitat extremes (Prater, 1985); a case in point, chital are absent from India's extremely moist Northeast region and are replaced by another *Axis* species, the hog deer *Axis porcinus*.

Although chital overlapped considerably with sambar for much of the year, sambar, unlike chital, showed a consistent preference for browse throughout the year (Fig. 3.2). Sambar 'niche breadth' was found to be as high as that of elephant (Table 3.2) and their extensive use of the study area hardly changed between the seasons (Figs. 3.3c-d). All of the above together suggest that sambar are capable of satisfying their metabolic requirements from a variety of habitats.

In addition to the evidence for our first hypothesis, our results also provided evidence to support our second hypothesis, which is that elephant 'niche breadth' would be the highest among the species (Table 3.3) and its overlap with that of the other species would be high during both seasons (Table 3.4). Also, finding elephants to be mixed feeders (Fig. 3.2) substantiated findings from earlier studies in the study area that also found elephants to be mixed-feeders (Sukumar 1990, 1992). Interestingly our results showed that gaur niche breadth was the narrowest among the four species. Also, although gaur 'niche breadth' with respect to the entire study area did not vary in size between seasons (Table 3.3), gaur showed a preference for different regions in different seasons. Speaking to local forest officials it appears that the near absence of gaur—except for a few individual old males and a herd or two—from the eastern (driest) part of the study area is an annual phenomenon. Therefore, it appears that gaur follow a local cyclic migration synchronized with the cyclic rainfall pattern, grazing in the dry deciduous region during the wet season and grazing in the moist deciduous region in the dry season (Figs. 3.3e-f).

Although the dry deciduous region received less rainfall and water bodies were stagnant, in contrast to the higher rainfall and flowing rivers in moist deciduous region (Table 3.2), water was available for consumption by gaur in the both habitats in the dry season. Also, the area that gaur were found in during the wet season was predominantly short-grass habitat, habitat that does not provide increased cover for gaur despite the increased grass growth in the wet season. Based on the above two facts, it is therefore unlikely that seasonal habitat selection by gaur is a function of ensuring access to water or minimizing predation risk.

Instead, the selection of habitat by gaur was a likely function of forage availability. Our results showed that grasses made up the majority of gaur diet throughout the year. This preference to graze by gaur is consistent with Hoffman's (1989) classification of large Bovini species as bulk feeders (grazers) and is similar to what has been found of other Bovini species like the American bison *Bison bison* (Knapp *et al*. 1999) and African buffalo (Sinclair, 1977; Prins, 1996); the European bison *Bison bonasus*, however, is a mixed feeder (Krasinska & Krasinski, 2007).

The very narrow 'niche breadth' of gaur in both seasons, however, suggest that gaur were probably being selective. The obvious question then is "What resource parameters were the gaur selecting for?" None of the habitat parameters measured had a significant correlation with gaur habitat preference. The field study area has historically had seasonal variation in plant quality, and at the same time is historically well known for its gaur population. It is therefore obvious that that guar have learned how to optimize the use of the spatial heterogeneity of available grass quantity and quality (Boone *et al.*, 2006). This offers one explanation for the seasonal habitat selection by gaur in the absence of strong correlations between (relevant) habitat parameters, like grass cover and height, and gaur habitat occupancy.

The absence of strong correlations between gaur habitat selection and habitat parameters also suggests that either the scale at which the habitat parameters were measured was too coarse, or that the habitat variables measured were not relevant. One example in support of the latter: the higher rainfall and running streams in the moist deciduous region meant a higher probability of live herbaceous biomass in the moist deciduous, than the dry deciduous region, during the dry season. Multiple naturalist observations, and a study of collared gaur in Malaysia (Conry, 1989), have recorded that gaur seek out riverine habitats to forage. Therefore, the moist deciduous region was probably better suited for gaur in the dry season than the dry deciduous region.

Although the grid-based survey did not detect any relevant habitat correlates of species presence, it revealed that in areas blanketed by the invasive *Lantana camara* (like in the dry deciduous tourism zone of Bandipur; Table 3.2) all three ruminant species were near absent and that elephants used these areas only marginally. *Lantana*-blanketed areas offer few understory palatable resources besides lantana itself, which is a non-preferred source of nutrition for large herbivores. The further expansion of this low-nutritious invasive appears to have the potential to impact resource availability and maybe the conservation of large herbivores (Sharma *et al*., 2005). There is, therefore, an urgent need to understand the exact impact that the presence and spread of this invasive species would have on the foraging ecology of large herbivores.

In conclusion, our results showed that it is was easier to predict grass:browse in the diets of some species (chital and elephant) but not of others (sambar and gaur) based on body mass based principles. The results also helped satisfying the goals of the study, which were to add to the empirical evidence from outside Africa to support large herbivore ecology theory based on body mass principles, and to help better understand foraging ecology of large herbivores in India. Also, the study area is part of the Nilgiri biosphere, an area with the distinction of supporting Asia’s highest wild herbivore biomass densities (Karanth, 1992), which in turn supports highest densities of large carnivores like tiger *Panthera tigris*, leopard *Panthera pardus*, and dhole *Cuon alpinus*. This study, therefore, which helps improve our understanding of large herbivore ecology in the Nilgiri Biosphere area, benefits the long-term conservation of not only large herbivore species conservation but also of that off endangered large carnivore species.

4

Why some species time their annual parturition with high plant quality availability? - the impact of body mass

Farshid S. Ahrestani, Frank van Langevelde, Ignas M.A. Heitkönig and Herbert H.T. Prins

Abstract

Seasonal variation in forage availability is understood to affect the annual timing of parturition in large herbivores. Also, body size is integral to a herbivore species' forage quantity and quality requirements. We found in India—where forage availability varies seasonally—that chital *Axis axis* exhibit seasonality in parturition, but the larger gaur *Bos gaurus* does not. We hypothesized that the difference between chital and gaur parturition could be explained by body size. We developed a model to simulate changes in leaf biomass and nitrogen content based on plant available moisture and nutrients and calibrated our model with field data. Our results show that the minimum forage nitrogen content required by lactating gaur was available throughout the year but that the minimum forage nitrogen content required by lactating chital were available for less than 40% of the year chital, i.e., during the early wet season. Nitrogen is the only element with requirements that scale to ¾, rather than a linear, exponential allometric function and therefore is the only element whose requirement varies between species of different body mass. The spread of chital births over a duration of three to four months implies low synchrony and suggests a low impact of predation on the timing of chital parturition. As monsoonal rain exhibits annual temporal variation, we also analyzed our model under different rainfall patterns while keeping the total annual rainfall constant. Results, however, with respect to these different patterns did not vary. This insensitivity for the variable rainfall pattern lends support to our hypothesis that body size offers a possible explanation as to why breeding cycles of different large herbivores species differ.

Introduction

Many animals live in environments where the availability and quality of food follow cyclical patterns of seasonal variation. In the temperate zone, food of adequate quantity is available only during the summer and not in winter; in tropical regions with seasonal rainfall, food abundance during the wet season is replaced by scarcity during the dry season. This ‘seasonality’ in food availability is understood to influence the timing of parturition of mammalian herbivores (Rutberg, 1987; Wittemyer *et al*., 2007). The ‘seasonality’ in parturition synchronized with durations of optimal food availability is understood to either support the increased energetic and nutritional requirements of lactating females (Prins, 1996; Gaillard *et al*., 2000), maximize the growth rate of neonates to enhance their predator avoidance (Clutton-Brock *et al*., 1982), or replenish maternal reserves for future reproduction (Bronson, 1985; Keech *et al*., 2000). The ‘seasonality’ of a species’ parturition is different from the synchrony of births. Synchrony refers to the length over which births occur within a population (Post, 2003) and was highlighted in mammals by Estes’ (1976) pioneering study which showed that the high synchrony of births within a wildebeest population could be interpreted as predator swamping, i.e., reducing the risk of an individual young by increasing potential prey per predator. The ‘predation hypothesis’ also includes the added benefit that neonates derive from being born into congregating groups of vigilant mothers during the calving peak (Rutburg, 1987; Bøving & Post, 1997). The ‘predation hypothesis’, however, is not mutually exclusive from the ‘seasonality hypothesis’; in the case of the wildebeest population, the time that they choose to calve during the year does coincide with the period of highest plant quality.

Studies have provided evidence to support the ‘seasonality hypothesis’ in herbivores in the temperate zone (Post & Stenseth, 1999; Post *et al*., 2003; Barboza & Reynolds, 2004; Langvatn *et al*., 2004; Loe *et al*., 2005). In the tropics, studies from Africa have shown that small and medium sized herbivores follow breeding cycles as well (Western, 1979; McNaughton & Georgiadis, 1986): mating occurs at the late wet or early dry season, and after a seven to nine month gestation period, parturition peaks during the early wet season. In Africa, the parturition peak of large herbivores in the early wet season coincides with the period of highest plant quality (Mduma *et al*., 1999), which supports the idea that the ‘seasonality’ of parturition—especially for smaller sized herbivores—is related to plant quality more than to plant biomass in the tropics (Olff *et al*., 2002). Also with limited photoperiodic influence on oestrous cycles in the tropics, the timing of ovarian activity/parturition cycles of small and medium sized tropical herbivores likely has evolved to satisfy the increased nutritional demands of females in late pregnancy and early lactation to nurture their offspring and themselves (Western, 1979; Bronson, 1989; Owen-Smith *et al*., 2005).

In much of tropical India forage production follows a seasonal/monsoonal rainfall regime. Asia’s largest bovid species the gaur *Bos gaurus* (600 kg) has a gestation period of 9 – 9.5 months, which lies within the gestation period range of African species that follow the ‘dry season mating-wet season parturition’ pattern described above. It has been suggested, though, that gaur do not have a well defined parturition peak and calve throughout the year (Schaller, 1967). A smaller sympatric herbivore species of the gaur, chital *Axis axis* (50 kg)—whose eight month gestation period also lies within the range of species that display ‘dry season mating-wet season parturition’—does exhibit seasonal annual parturition (Schaller, 1967; Raman, 1998).

The timing of breeding cycles of tropical mammalian herbivores has not been related to body size so far. Body mass based foraging theory suggests that forage quantity and quality requirements of chital and the ten times heavier gaur are different (Kleiber, 1932; Demment &

Van Soest, 1985; Owen-Smith, 1988; Van Soest, 1994; Olff *et al*., 2002). The differences in forage requirements between species are accentuated when comparing the requirements of individuals of these species that demand high quality forage, such as females during late pregnancy and lactation and young calves. Also, a greater proportion of megaherbivores—a guild for which the gaur is the next eligible species—exhibit perennial parturition than the proportion of smaller species that do so (Laws *et al*., 1975; Owen-Smith, 1988) (Appendix 4.1). We therefore hypothesized that the difference in the impact that body mass has on the forage requirements of chital and gaur, particularly lactating females, would help explain why chital calve every year at the same time, and gaur do not.

As base data for testing our hypothesis, we collected field data on the timing of parturition of both chital and gaur throughout the year. We modelled the seasonal pattern in the availability of primary production nutrition based on plant available moisture and nutrients. We calibrated our model with measurements of available food quantity (grass biomass) and quality (N content of grass leaves) on different occasions during the year. Finally, based on known relationships between herbivore body size and nutritional requirements we investigated whether the seasonal variability in food availability and quality forces smaller species (like chital) and not larger species (like gaur) to time their parturition with the primary production cycle so as to satisfy the increased nutritional demands of lactating females. As annual variation in monsoonal rain exists, we also analyzed our model to see whether lactating females could meet their requirements for three different rainfall regimes: (i) the observed bimodal rainfall pattern containing the Southwest and Northeast monsoon, (ii) the rainfall pattern with a reduced Northeast monsoon, and (iii) with a reduced Southwest monsoon.

Model

Motivation for model - Breeding data of chital and gaur

We collected field data to compare the calf to female ratio of chital and gaur between March 2006 and August 2007 in two contiguous Tiger Reserves in South India, Mudumalai (329 km^2; $11^{o}32^{'}$-$43^{'}$N, $76^{0}22^{'}$-$45^{'}$E) and Bandipur (880 km^2; 11^{o}36-$57^{'}$N, 76^{o}13-$52^{'}$E). Most data were collected from a 200 km^2 study area (Fig. 1.1) that was split equally between the two Reserves. Given the difficulty in observing the animals in forested areas, and the fact that both species were more tolerant of humans in vehicles than on foot, the majority of data were collected using an open-topped jeep while systematically sampling the study area along its 50 km road network. The sampling effort for the study period exceeded 2500 km and was restricted mainly to dawn and dusk, times when both species were both active and visible.

We found chital parturition to peak during February-May (Fig. 4.1). Gaur appeared to calve throughout the year; the spike of the 100% parturition rate in May 2007 was based on a sample size that included only five females. In general, other studies have also shown that gaur do not have a definite annual parturition peak, and in North India the probable peak period for gaur parturition has been reported as October-January (Schaller, 1967).

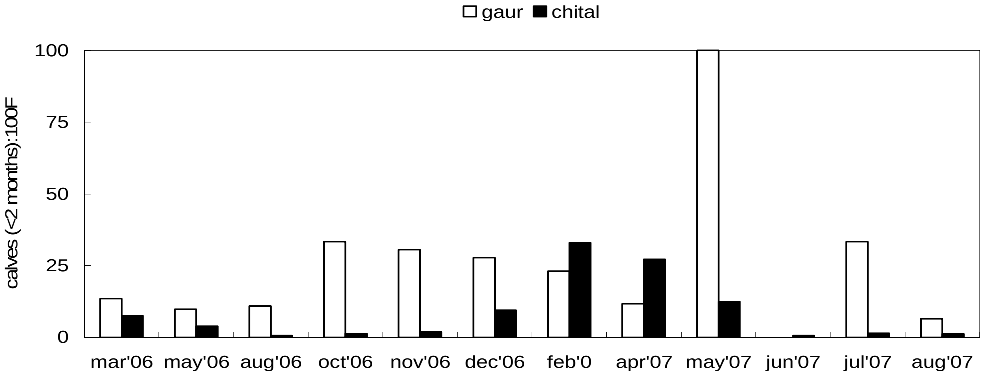


Fig. 4.1. Comparison of the ratio of calves(<2 months)<):100 female found for gaur *Bos gaurus* and chital *Axis axis* in Mudumalai and Bandipur National Parks, South India, March 2006–August 2007.

Model definition

We developed a simple model to simulate changes in leaf biomass and nitrogen content in time steps of one month (Appendix 4.2 lists the parameters used in the model, their symbols, interpretation, units and values). We modelled the growth of leaf biomass to include losses due to senescence and grazing. We assumed that local plant growth is limited by available soil nitrogen and moisture (Chapter 2). We modelled growth of only grass leaves as they are preferred by herbivores (Van Langevelde *et al.*, 2008). The change in leaf biomass (P in g m^{-2}) was modelled as

$$\frac{\mathrm{d}P}{\mathrm{d}t} = r\,n\,P - g(P)P - b\,h\,P \qquad (1)$$

where n is the plant available soil moisture content (PAM), r the specific growth rate of leaf biomass per unit of available soil moisture, $g(P)$ the loss rate due to senescence, h the herbivore density, and b the specific consumption rate of the herbivores. We assumed a density-dependent loss rate due to senescence so that $g(P) = a\,P$, where a is the specific density-dependent loss rate.

Similar to the seasonal pattern of leaf biomass, the content of nutrients in this biomass increases due to uptake by the plants and decreases when the plant looses leaves as a result of both senescence and grazing. Uptake of nutrients is modelled as a saturating function of aboveground biomass as we assume that older grasses invest more in structural material (stems) and less in organs to acquire resources (Beever *et al.*, 2000). The change in nitrogen content (N in g m^{-2}) is

$$\frac{\mathrm{d}N}{\mathrm{d}t} = u\frac{P}{P+k}S - m\,N - b\,h\,N \qquad (2)$$

where u is the maximum uptake rate of nutrients, k the leaf biomass where the uptake of nutrients is half of u (half saturation constant), S the available soil nutrients (PAN), m the specific loss rate of nutrients due to senescence. We assume that a nutrient pulse F (temporarily increasing S) is available from accumulated plant detritus and animal dung at the beginning of the wet season that benefits the growth of young shoots, which are very nutritious for herbivores (McNaughton, 1985; Scholes & Walker, 1993).

Model calibration

To calibrate the model, we measured live leaf biomass from August 2006 - July 2007 on a grassland located in a wildlife resort bordering Mudumalai Tiger Reserve, South India (N 11^{o}55’, E 76^{o}63’; Fig. 1.1). Mudumalai hosts a diverse assemblage of herbivores including Asian elephant (*Elephas maximus*), gaur (*Bos gaurus*), sambar (*Cervus unicolor*), chital (*Axis axis*), muntjac (*Muntiacus muntjak*), four horned antelope (*Tetracerus quadricornis*) and Indian spotted chevrotain (*Moschiola meminna*). The study site received a monsoonal driven rainfall cycle that included a wet (May – November) and a dry (December – April) season. The wet season received precipitation from two sources: the Southwest monsoon (May – August) followed by the Northeast monsoon (September – November). Rainfall in Masinagudi (2 km north the experiment site) during our study period (July 2006 – July 2007) was 730 mm, below the last 15 year (1991-2005) average of 860 mm. Mean annual temperature was 16 – 18^{o}C, reaching its maximum of 28 – 30^{o}C in April-May and dropping to its minimum of 5 – 6^{o}C in December-January. Soils were slightly acidic with low nitrogen content, and were sandy loam on the surface with a gravelly clay substrate (Chapter 2).

While keeping annual rainfall the same, we also tested our model under different rainfall regimes: a reduced Northeast monsoon (yearly average of 825 mm) and a reduced Southwest monsoon (yearly average of 852 mm).

Results

Using ordinary least square regression, we fitted a nonlinear model to represent rainfall over the year (Fig. 4.2). We *ln*-transformed rainfall and fitted a polynomial function (up to the 6th power) with month as independent variable ($n = 12$, adjusted $R^2 = 0.99$, constant = -5.631 ($t = -16.175$, $p < 0.001$), and regression coefficients for month = 5.572 ($t = 18.784$, $p < 0.001$), for month^2 = -1.021 ($t = -14.245$, $p < 0.001$), for month^3 = 0.064 ($t = 12.055$, $p < 0.001$) and for month^6 = -7.423×10^{-6} ($t = -10.088$, $p < 0.001$). The regression coefficients month^4 ($t = 1.028$, $p = 0.344$) and month^5 ($t = 1.146$, $p = 0.295$) could not be added to the model. This relationship was used as PAM in the model (equation 1) to predict the annual pattern in forage availability as the amount of leaf biomass (Fig. 4.3), and forage quality as the amount of nitrogen content in leaves (Fig. 4.4).

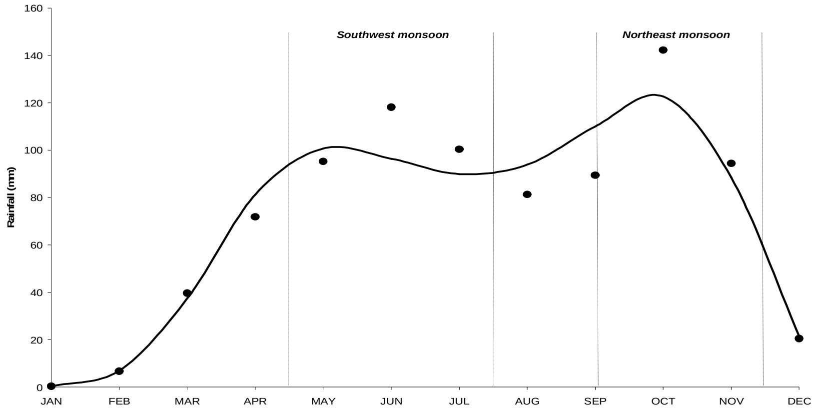


Fig. 4.2. Measured rainfall (dots) and the fitted relationship (see text for statistical details) to be used in the model.

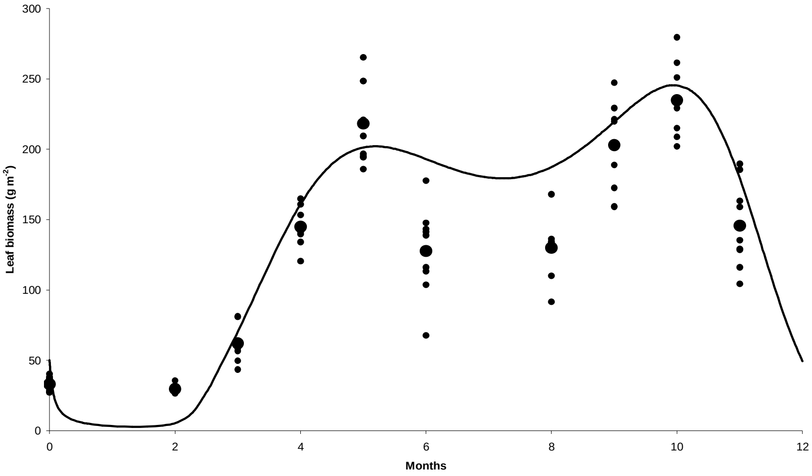


Fig. 4.3. Measured (dots, large dots represent the means) and simulated amount of leaf biomass during the year (0 = January).

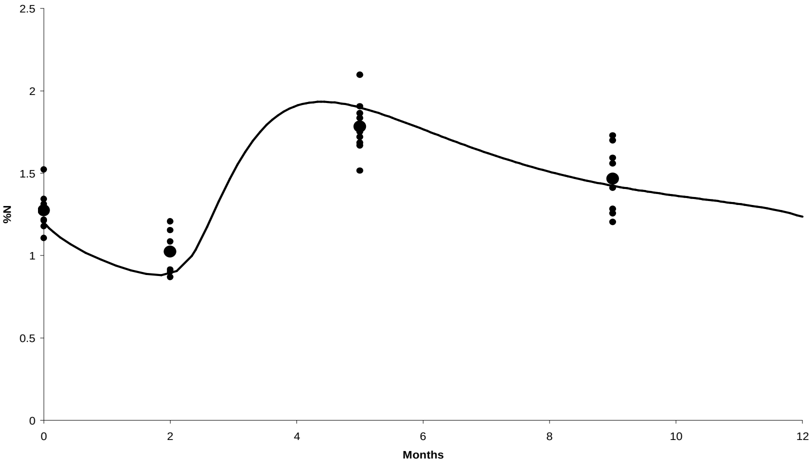


Fig. 4.4. Measured (dots, large dots represent the means) and simulated leaf nitrogen content during the year (0 = January)

The daily requirements for maintenance, pregnancy and lactation for chital and gaur are derived from known allometric relationships (Appendix 4.3). Assuming that ruminant herbivores consume about 2% of their body mass on a dry matter basis every day (Murray, 1995), we can estimate the daily required nutrient concentration as the daily requirements divided by the daily intake. This means that chital need 1.22% and gaur 0.66% N for maintenance; chital need 1.47% and gaur 0.79% N for pregnancy; and chital need 1.89% and gaur 1.02% N for lactation. For the other elements there is no difference in the requirement between the two species, as body mass is raised to the power 1 and hence the multiplier of body mass for these requirements is a linear relationship (for example, chital and gaur both need 0.1% P for maintenance). Herbivores can meet their daily energy requirements by adapting foraging times (Shipley *et al.*, 1994); during periods of low forage availability, herbivores can forage longer to meet their energy requirements. We assume therefore that herbivores in our study area meet their daily energy requirements throughout the year, and postulate that the differences in timing of parturition between chital and gaur can be explained by differences in nitrogen supply.

Comparing the daily requirements with that of the simulated available leaf nitrogen content shows that gaur meets its requirements for all activities (maintenance, pregnancy and lactation) throughout the year. However, for chital this pattern is different: it meets its requirements for maintenance during around 86% of the year, for pregnancy around 79% and for lactation only 37% of the year (Fig. 4.5).

For both the modified rainfall regimes (a reduced Northeast, and a reduced Southwest, monsoon) we again fitted a polynomial curve with month as independent variable (Fig. 4.5). With these rainfall scenarios, we simulated leaf biomass and the leaf nitrogen content over time (Fig. 4.5). In both these two scenarios, gaur can meet their requirements for all activities throughout the year. For chital this pattern is different: chital meet their requirements for maintenance during around 86% of the year (for both scenarios), for pregnancy between 75-78% (for both scenarios) and for lactation 39% (scenario reduced Northeast monsoon) and 31% (scenario reduced Southwest monsoon) of the year.

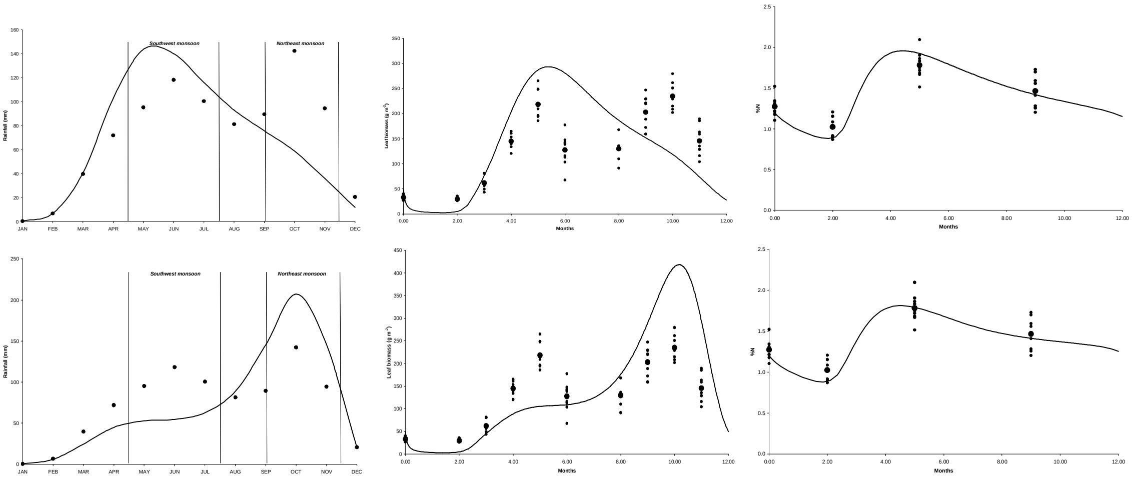


Fig. 4.5. Measured (dots, see Figs. 4.3, 4.4, 4.5) and simulated rainfall, leaf biomass and leaf nitrogen conent during the year for the two scenarios: rainfall pattern with a reduced Northeast monsoon (top row panels) and with a reduced Southwest monsoon (bottom row panels). For both scenarios, we fitted polynomial models using *ln*-transformed rainfall data. For the reduced Northeast monsoon ($n = 12$, adjusted $R^2 = 0.97$), we found the constant = -5.386 ($t = -8.337$, $p < 0.001$), and the regression coefficients for month = 5.175 ($t = 9.402$, $p < 0.001$), for month^2 = -0.860 ($t = -6.466$, $p < 0.001$), for month^3 = 0.048 ($t = 4.898$, $p = 0.002$) and for month^6 = -4.727×10^{-6} ($t = -3.462$, $p = 0.011$). The coefficients month^4 ($t = 1.354$, $p = 0.225$) and month^5 ($t = 1.546$, $p = 0.173$) could not be added to the model. For the rainfall pattern with a reduced Southwest monsoon, we found the regression model ($n = 12$, adjusted $R^2 = 0.99$) with the constant = -5.212 ($t = -16.938$, $p < 0.001$), and the coefficients for month = 5.283 ($t = 20.150$, $p < 0.001$), for month^2 = -1.040 ($t = -16.410$, $p < 0.001$), for month^3 = 0.071 ($t = 15.126$, $p < 0.001$) and for month^6 = -9.586×10^{-6} ($t = -14.737$, $p < 0.001$). The coefficients month^4 ($t = 1.354$, $p = 0.225$) and month^5 ($t = 1.546$, $p = 0.173$) could not be added to the model.

Discussion

Mammals do appear to respond strongly to dietary nutrients in seasonal environments and the availability of nitrogen is considered to be a key driver of forage selection by herbivores, especially for smaller herbivores (Prins & Beekman, 1989; Van Soest, 1994). Our results support this idea by highlighting the contrast in the time periods when available plant nitrogen is above the minimum required by lactating females (i.e., individuals in a population that have the highest nutritional demands) of gaur and chital; the entire year for gaur but only four months for chital. These results suggest that gaur are not constrained to time their parturition to satisfy individual nitrogen requirements, which provides one explanation as to why gaur do not exhibit 'seasonality' in their parturition.

The timing of the parturition peak in chital during our study, February-April, shows that there was a high overlap of the early wet season, the season when available plant quality was above the minimum required by lactating chital females. When meeting their nitrogen demands, these females benefit by improving their lactation ability and milk quality, which helps increase pre-weaning calf survival (Clutton-Brock *et al*., 1982; Rognmo *et al.*, 1983) and helps maintain the mother's body condition and replenish her reserves for future reproduction (Bronson, 1989; Keech *et al*., 2000). The December to March annual peak found for other chital populations (Schaller, 1967 [Kanha, India]; Johnsingh, 1985 [Bandipur, India]; Raman, 1998 [Guindy, India]) suggests that the 'seasonality' of the parturition in these populations would help replenish maternal reserves for future reproduction (Bronson, 1989; Keech *et al*., 2000) and ensure continued growth of neonates (Clutton-Brock *et al*., 1982) more than helping to satisfy the requirements of lactating females.

Because nitrogen is the only element whose requirement is determined by a ¾, rather than a linear, exponential allometric function, it is therefore the only element whose requirement varies between species of different body size. The linear allometric requirement functions of other nutrients–like P, K, Ca and Na–means that variation in their availability impacts species of different body mass equally. This, however, does not mean that other nutrients are not important for maintenance, pregnancy or lactation (Van Soest, 1994).

In addition to the seasonal variation in nutrient availability, the seasonal variation in vegetative quality–as a function of the fibre and lignin content–are also critical forage selection criteria by large herbivores (Prins & Beekman, 1989). Body mass plays an important role with respect to fibre and lignin content too, as smaller species (chital) are less tolerant of forage high in fibre and lignin content than are larger species (gaur). Both fibre and lignin are at their lowest during the early wet season, and then increase over time till the next rains (Prins, 1988; Beever *et al.*, 2000). The pattern of seasonal variation in forage and lignin availability is cyclic and is similar to the seasonal cyclic pattern of nitrogen content availability. It is worth noting that while nitrogen content decreases, fibre and lignin content increase, which highlights the inverse relationship of forage quantity and quality. When comparing the different rainfall scenarios, the insensitivity for the exact rainfall pattern supports our conclusion that body size can explain differences in breeding cycles in large herbivores. For constant total amount of rainfall, similar peak in parturition peak in chital can be expected, whereas requirements for lactating female gaur are met throughout the year.

Although data appears to support 'seasonality' of chital parturition, the lack of data on the variation in predation rates on chital and gaur makes it difficult to comment on whether the timing of their parturition can be explained by the 'predator hypothesis'. The extended period of

2 – 4 months of the peak of chital parturition implies, however, low synchrony and suggests that the chital population do not engage in predator swamping.

In conclusion, we present an explanation based on body mass based principles as to why species of different body mass have different reproductive behaviour. We demonstrated that plant nitrogen content can be a seasonally limiting factor for smaller species like chital but not for larger species like gaur. Also, the extended parturition peak of chital implies low synchrony in chital parturition. And finally, although we focused on the variation of nitrogen, the seasonal variation of either fibre or lignin content of the vegetation could influence the variation observed between reproductive behaviour of herbivores of different body mass.

Appendix 4.1. Birthing characteristics of tropical large herbivores from Africa, Asia and Australia (Estes, 1991; Kingdon, 1997)

Common Name	Scientific name	Body mass (kg)	Gestation period (months)	Birthing period
Muntjac	*Muntiacus reevesi*	15	7	Seasonal (dry)
Common duiker	*Sylvicapra grimmia*	15	6.5	Perennial
Black wallaby	*Wallabia bicolor*	15	8	Seasonal (wet)
Thomson's Gazelle	*Gazella thomsonii*	20	6	Seasonal (wet)
Four-horned antelope	*Tetracerus quadricornis*	20	7.5	Seasonal (wet)
Blackbuck	*Antilope cervicapra*	30	5.5	Seasonal (wet)
Antilopine wallaby	*Macropus antilopinus*	35	(marsupial)	Seasonal (late dry)
Hog deer	*Axis porcinus*	45	6	Seasonal (wet)
Eastern grey kangaroo	*Macropus giganteus*	50	(marsupial)	Seasonal (wet)
Chital	*Axis axis*	50	7	Seasonal (wet)
Red kangaroo	*Macropus rufus*	60	(marsupial)	Seasonal (wet)
Southern reedbuck	*Redunca arundinum*	80	7.5	Seasonal (wet)
Nyala	*Tragelaphus angasii*	110	7	Perennial (wet)
Topi	*Damaliscus lunatus*	140	8	Seasonal (late dry)
Hartebeest	*Alcelaphus buselaphus*	170	8	Perennial (wet)
Barasingha	*Rucervus duvaucelii*	180	8	Seasonal (wet)
Common wildebeest	*Connochaetes taurinus*	180	8	Seasonal (early wet)
Sambar	*Cervus unicolor*	200	8	Seasonal (wet)
Nilgai	*Boselaphus tragocamelus*	200	8	Seasonal (wet)
Greater kudu	*Tragelaphus strepsiceros*	210	9	Seasonal (wet)
Sable	*Hippotragus niger*	270	8	Seasonal (late wet)
Grevey's zebra	*Equus grevyi*	400	13	Seasonal (early wet)
Eland	*Taurotragus oryx*	450	9	Perennial (early wet)
African buffalo	*Syncerus caffer*	550	11	Seasonal (wet)
Gaur	*Bos gaurus*	600	9.5	Perennial
Black rhino	*Diceros bicornis*	1800	16	Perennial
Asian elephant	*Elephas maximus*	4000	22	Perennial
African elephant	*Loxodonta africana*	5000	22	Seasonal (wet)

Appendix 4.2. Symbols used in the model, their interpretation, units and values.

Symbols	Interpretation	Units	Values	Sources
P	aboveground live leaf biomass	g m^{-2}	0-300	Field measurements
N	nutrient content of leaves	g m^{-2}	0-2.5	Field measurements
n	plant available soil moisture content (PAM)	mm d^{-1} $month^{-1}$	0-150	Field measurements
r	specific growth rate of plant biomass per unit available soil moisture	mm^{-1}	0.6	Gambiza *et al.* (2000)
h	herbivore density	g m^{-2}	10	Pers. observation Ahrestani
b	specific consumption rate of herbivores	m^2 g^{-1} d^{-1} $month^{-1}$	0.02	Murray (1993)
a	specific density-dependent loss rate	m^2 g^{-1} d^{-1} $month^{-1}$	0.3	Gambiza *et al.* (2000)
u	maximum uptake rate of nutrients	m^2 g^{-1} d^{-1} $month^{-1}$	0.1	Risser and Parton (1982)
k	plant biomass where the uptake of nutrients is half of u	g m^{-2}	25	Estimated
s	available soil nutrients (PAN)	g m^{-2}	8	De Mazancourt *et al.* (1999)
m	specific loss rate of nutrients due to senescence	$month^{-1}$	0.3	Similar as a
F	nutrient pulse at beginning of wet season	g m^{-2}	15	De Mazancourt *et al.* (1999)

Appendix 4.3. Nutritional requirements of chital and gaur per day.

Activity	Nutrient (unit)	Allometric function	Chital (50kg)	Gaur (600kg)	Source
Maintenance	Energy (kJ d^{-1})	$293 \times W^{0.75}$	5510	35521	2
	N (g d^{-1})	$0.65 \times W^{0.75}$	12.22	78.80	2
	P (g d^{-1})	$0.02 \times W^{1.0}$	1.00	12.00	2
	Ca (g d^{-1})	$0.024 \times W^{1.0}$	1.20	14.40	2
	Na (g d^{-1})	$0.009 \times W^{1.0}$	0.45	5.40	2
Pregnancy	Energy (kJ d^{-1})	$351 \times W^{0.75}$	6600	42552	guesstimate
	N (g d^{-1})	$0.78 \times W^{0.75}$	14.67	94.56	1
	P (g d^{-1})	$0.038 \times W^{1.0}$	1.90	22.80	1
	Ca (g d^{-1})	$0.047 \times W^{1.0}$	2.35	28.20	1
	Na (g d^{-1})	$0.013 \times W^{1.0}$	0.65	7.80	1
Lactation	Energy (kJ d^{-1})	$440 \times W^{0.75}$	8273	53342	guesstimate
	N (g d^{-1})	$1.01 \times W^{0.75}$	18.99	122.44	1
	P (g d^{-1})	$0.08 \times W^{1.0}$	4.00	48.00	2
	Ca (g d^{-1})	$0.096 \times W^{1.0}$	4.80	57.60	2
	Na (g d^{-1})	$0.036 \times W^{1.0}$	1.80	21.60	2

Sources:

1. Agricultural Research Council Working Party, 1980
2. Prins & Van Langevelde, 2008

Notes:

- The calculation for energy requirement for pregnant and lactating females was estimates as 20% & 50% greater than basal requirement.
- The calculation for N requirement for pregnant females was calculated as 20% greater than basal requirement, but for lactating females the N requirement was calculated as the average of the requirement of cows weighing 500 kg and producing 5 – 40 litres of milk with 40 g/kg fat.

5

Age and sex determination of gaur *Bos gaurus*

Farshid S. Ahrestani, Herbert H.T. Prins

Abstract

The gaur (*Bos gaurus* Smith 1827) is a poorly understood species. One reason for this is the lack of reliable data on how to age and sex gaur. Based on a two year study of individuals of known age and sex in Mysore Zoo, South India, we analyzed growth patterns and age-specific morphological differences, and developed visual references from birth to the age of 10 years, for both sexes of gaur. Till the age of 15 months, gaur are difficult to sex in the field. The sex of gaur between 15-36 months is best distinguished by the characteristics of their horns. The size and shape of the horns differ between the sexes, and the amount of white on the horns increases with age in both sexes. Above the age of three years, other morphological differences besides the horns, like body colour and the presence/absence of the dorsal ridge and dewlaps found in males, can also be used to sex gaur.

Introduction

The gaur (*Bos gaurus* Smith 1827)–despite its lofty status as Asia's largest bovid species and a likely megaherbivore (Owen-Smith, 1988), and in spite of its 'threatened' Red List status (IUCN, 2007) and imminent danger of extirpation within much of its Southeast Asian range (Duckworth & Hedges, 1998)–is, surprisingly, a poorly understood species.

In contrast to the gaur, other similar sized phylogenetically related Bovini species like the North American bison *Bison bison* (Lott, 2002), African buffalo *Syncercus caffer* (Sinclair, 1977; Prins, 1996), and European bison *Bison bonasus* (Krasinska & Krasinski, 2007) are well studied. One major reason for this is the availability of detailed field-tested age and sex determination data of these species: McHugh (1958) and Fuller (1959) still remain the major references for detailed age and sex specific morphological characteristics for North American bison; Grimsdell (1973) and Sinclair (1977) are the major references for African buffalo; and the more recent comprehensive Krasinska and Krasinski (2007) monograph is the definitive resource for European bison. The availability of this information for 50 years of North American bison, and the 30 years of African buffalo, paved the way for numerous other studies that have resulted in both being well understood species (e.g. Lott, 2002; Prins, 1996; respectively).

To improve understanding of gaur biology, particularly its population biology and demography, there is therefore first a need for reliable data to help identify gaur by age and sex. Schaller (1967) did define different size classes for both sexes of gaur. He admitted, however, that his was a "crude and relative age scale" and suggested that "an accurate aging technique based, perhaps, on horn length and shape, as was used for the American bison by McHugh, would be more desirable". The lack of an update to this suggestion made over 40 years ago was a major motivation for this study.

Based on a two year study of India's largest captive gaur population housed in Mysore Zoo, South India, we present methods and data on how to age and sex free ranging gaur based on their morphological features.

Materials and methods

Captive populations with individuals of known age provide the ideal setting to study age-specific morphological growth patterns of a species. We studied India's largest captive gaur population housed in Mysore Zoo, Karnataka, from November 2005 to August 2007. This population originated from three wild individuals captured in nearby Bandipur Tiger Reserve, and had been separated into two sub-populations over a decade ago. During the study period we collected data on morphological characteristics of 28 different individuals of known age that included 16 females from birth to the age of 16 years, and 12 males from birth to the age of 11 years. We obtained heights of different aged gaur of both sexes by combining the absolute measurements of 12 different individuals photographed against scales painted on walls within their enclosures and the relative height differences between individuals photographed together. All photographs that provided measurements of the absolute height of different gaur were taken while standing at the same ground level of the individuals being photographed, and we used over 100 digital photographs of various group assemblages for our analysis.

We derived equations of the growth of shoulder height (the point on the dorsal ridge that aligns in a straight line with the fore leg) for both sexes using the Von Bertalanffy function (Von Bertalanffy, 1938; Hanks, 1972; Sinclair, 1977; Sukumar *et al*., 1988)

$$L_t = L_\infty \{1-\exp[-K(t-t_0)]\} \qquad (1)$$

where L_t = shoulder height at age t (years); L_∞ = asymptotic shoulder height; K = coefficient of catabolism; and t_0 = theoretical age at which the animal would have zero height. To calculate L_∞ we would require measurements at single year intervals for the entire age span. As this was not available, we assumed L_∞ to be marginally higher than the maximum measured height for each sex. To estimate t_0 and K we plotted the natural log of $[L_\infty/(L_\infty - L_t)]$ against age and fitted a linear regression; the intercept of the regression line was $-Kt_0$ and the slope K.

With the help of artists, and using both the absolute height measurements and the relative height differences between individuals of different ages, we developed sketches illustrating the different patterns in physical growth of male and female gaur from birth to the age of 10 years. In forested landscapes one often gets to see only the heads of gaur completely. We, therefore, also developed separate illustrations of only the head and horns of male and female gaur from birth to the age of 10 years using the ratios of different head and horns measurements made from photographs.

We tested and validated our findings using gaur individuals of know age and sex from the world's largest captive gaur population housed in Henry Doorly Zoo, Omaha, NE, USA, in July 2006.

Results

Body size

Height at shoulder was 170cm for the oldest and tallest male (11 years), and 142cm for the healthiest adult female (10 years). Growth in body size is similar in both sexes till the age of 15 months (Fig. 5.1). Females attain 96% of their adult height by three years (Fig. 5.1) and reach maximum adult size by five-six years, while males continue to grow in height and size past the age of 10 years (the oldest observed male lived 12 years).

For ages 0-10 years the Bertalanffy growth function derived for male gaur was

$$L_t = 175\ \{1-\exp[-0.28(t-3.2)]\}$$

and for female gaur was

$$L_t = 145\ \{1-\exp[-0.30(t-5.2)]\}$$

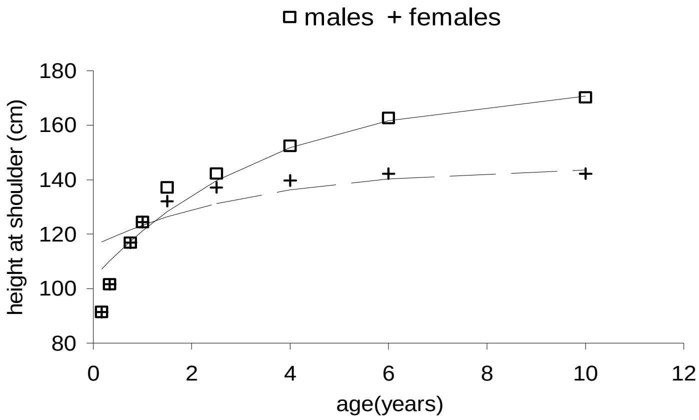


Fig. 5.1. Growth patterns of shoulder height of male and female *Bos gaurus* studied in Mysore Zoo, South India, 2005-2007 (see text for fitted regression lines).

Morphological characteristics of different age classes of male and female gaur

Based on height, size, and other morphological features we identified three initial discernable age classes (0-2 months, 3-5 months, and 6-15 months). In general, it is difficult to identify the sex of gaur in these age-classes.

(0-2 months) Calves at this age are easily distinguishable by their light orange-brown body coats. They have a white throat patch for the first few weeks, the insides of their legs above the knees are white, and their ‘white stockings’ are not yet visible. Horns, if visible, normally appear only as bumps on the head. Gaur at birth stand 62-67cm at the shoulder and grow 10-20cm in height, and 50% in body mass, in the first two months.

(3-5 months) Gaur in this age class are not much bigger than the previous age class, but the colour of their body coat has changed to a darker brown and their ‘white stockings’ become visible. Height at shoulder by the age of five months is at least 80cm. Horns are usually visible, are coloured black, and are less than 10-12cm long. Horns of males are normally longer than those of females, but this feature cannot be used to distinguish between the sexes. Besides trying to confirm the presence of a scrotum–which is difficult to observe in free ranging gaur of this age–no other visible morphological difference can be used to distinguish between the sexes in this age class.

(6-15 months) In this age class female and male gaur both grow significantly, equally, and reach two-thirds the height of adult females at the shoulder (Figs. 5.2a-b). Horns of males in this age class are longer, but still do not differ in shape from those of females. Again, the scrotum of males–which is difficult to observe in free ranging gaur in this age class too–is the only visible morphological difference that can be used to distinguish between the sexes in this age class.

Beyond the age of 15 months we identified five older age classes for males, and four for females, that can be distinguished based on morphological differences with an emphasis on horn characteristics.

(15-24 months) In this age class male and female gaur are similar in height and size and have grown to 80% of adult female body size and are 90% as tall as adult females at the shoulder (Figs. 5.2a-b). The anterior of male bodies, but not of females, begins to blacken by the age of two. However, what distinguishes the sexes apart are their horns. *Female horns*: reach 18-25cm in length, remain completely black, curve less away from the head–making the horns less apart from each other–and their ends point inwards (Fig. 5.3a). *Male horns*: reach nearly 30cm in length, curve spreading away from the head, and taper to sharp ends pointing upwards (Fig. 5.3b). An important change in the colour of horns–which is the whitening of gaur horns from the base up–begins for males at this age class; male horns are 20-25% white by the age of two years (Fig. 5.3b).

(2-3 years) Although males are bigger than females in this age class, it is best to differentiate between the sexes based on horn differences. *Females*: by the age of three years are 95% as tall at the shoulder, and are 80-90% as heavy, as adult females (Figs. 5.1, 5.2a). During this year their horns develop significantly in length and thickness, are 20-30% white, and have a semi-circular shape with ends pointing towards each other (Fig. 5.3a). *Males*: by the age of three begin to exceed the size of adult females (Figs. 5.1, 5.2). Their horns are significantly longer, thicker, and wider apart than those of females of the same age and males of the previous age class. Their horns are also 50-60% white with ends that still point upwards (Fig. 5.3b).

*(> 3 years***)** Gaur above the age of three can be considered adults and are normally easy to sex. *Females*: Do not grow much in height beyond the age of three years, but do so in body mass till the age of five-six years (Figs. 5.1, 5.2a). Their horns continue to get bigger, longer, and to curve

more inwards with increasing age (Fig. 5.3a). If the amount of white on a female's horns exceeds 80% it would be safe to assume that the female is old (>10 years). *Males*: (*3-5 years*) During these two years males continue to get bigger in size (Figs. 5.1, 5.2b) and their coats get blacker, beginning from the anterior moving back. The dorsal ridge begins to get more pronounced in size and mass. Their horns thicken along the entire length and begin to curve inwards at the ends, an important feature that distinguishing males in this age class from the previous age class. Their horn ends are less pointed and are 60-70% white by the age of five (Fig. 5.3b). (*>5 years*) Beyond the age of five, males can be called 'black bulls'. With advancing age, black bulls continue to increase in height and mass, their coats continue to blacken, their dorsal ridge continues to grow in height and thickness, their dewlaps continue to develop, the white on their horns continues to increases, and their horn ends continue to become more rounded and less pointed (Figs. 5.1, 5.2b, 5.3b). Males, with horns that are over 85% white and appreciably worn at the ends, can be considered old (>8 years).

Discussion

Although data for this study were derived from a captive population, the majority of this population's founding wild stock were still alive during the study. This underscores why we have little reason to doubt that growth patterns in wild gaur vary from those described in this paper.

Important findings of this study were that it is possible to sex gaur that are older than 15 months based on only horn characteristics, and that the amount of white on gaur horns is an important indicator of age in both sexes. Often only the heads of gaur are seen above the forest undergrowth, so a careful study of the shape, size, and colour of the horns are a field researcher's best identification tools. Often horn characteristics is all one can use to distinguish the sex of gaur that are 15-36 months, an age class in which there is little difference in body size between the sexes and distinguishing features like the dorsal ridge and dewlap of adult males are not yet developed. We recommend that it is best to use as many discernable morphological features as possible when classifying gaur and that it is always best to try and confirm the presence of a scrotum, especially when trying to identify the sex of young gaur.

Identifying the sex of adult gaur is normally straightforward. Beyond the age of five years, however, it is difficult to classify individuals in single-year age classes based on only morphological differences. Therefore, the best one can do is to classify adult gaur of both sexes into broad age classes. A potential alternate to determine the age of gaur could be through studying their dentition, similar to what Fuller (1959), Sergeant & Pimlott (1959), Grimsdell (1973), Høye (2006), and Margarido *et al*. (2007) have shown is possible with American bison, moose *Alces alces*, African buffalo, roe deer *Capreolus capreolus*, and white-lipped peccaries *Tayassu pecari* respectively. Using the wear of teeth as an indicator of age, however, is only suitable for classifying immobilized individuals and probably won't be an option available for most gaur field studies.

The differences in growth patterns and characteristics between male and female gaur horns are similar to what has been found of other Bovini species, particularly the North American bison (McHugh, 1958) and the European bison (Krasinska & Krasinski, 2007). Similar to gaur, the horns of males in both bison species are longer, thicker, and curve away more from the head (which sets them further apart) than the horns of females. The amount of white on a gaur's horns which provides an estimate of its age–a feature possibly also true in banteng *Bos javanicus*–is, however, not a feature present in the bison species.

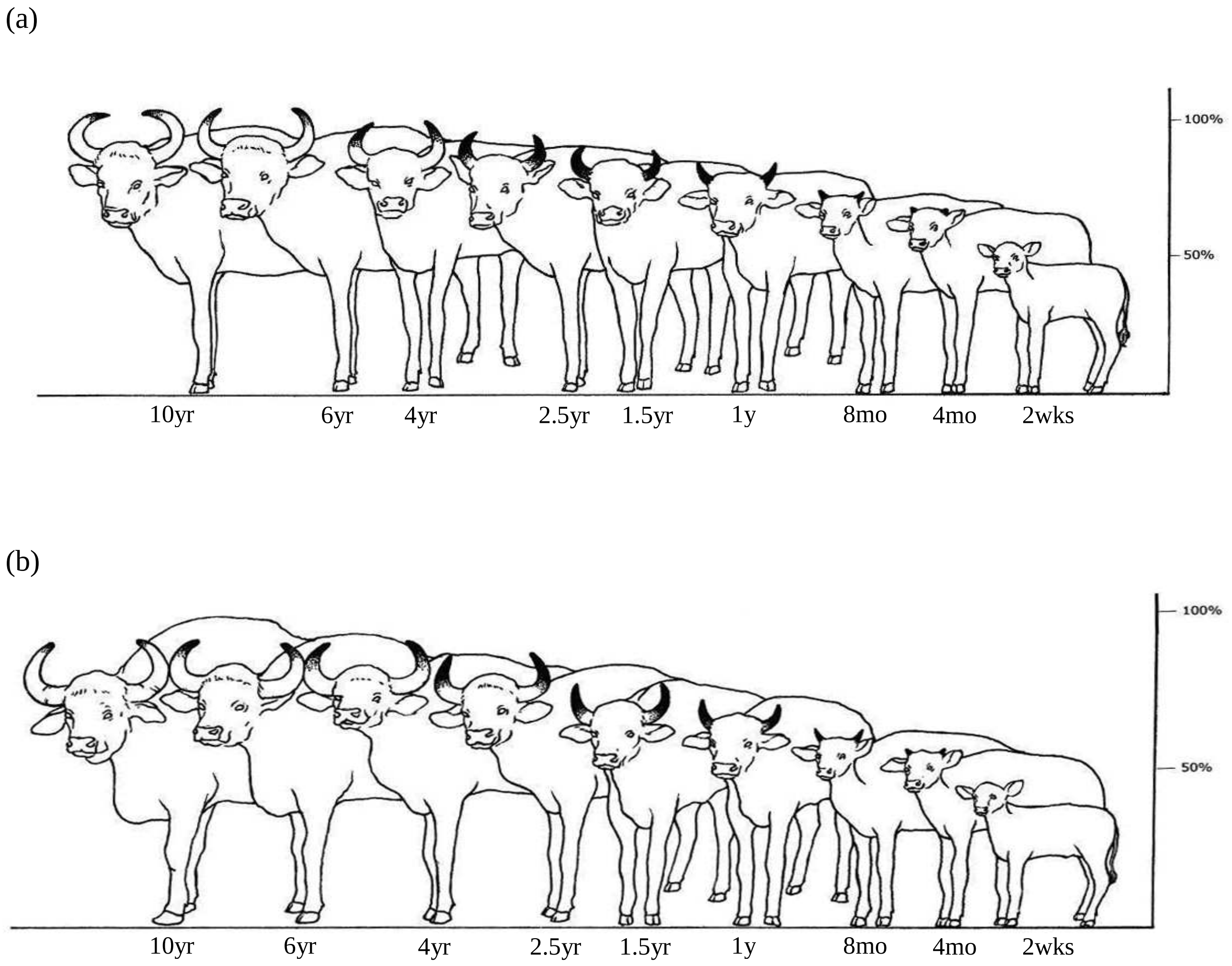


Fig. 5.2. Relative age-specific growth of (a) female and (b) male gaur *Bos gaurus* drawn from photographs of individuals of known age to a relative scale where 100% = shoulder height of 10 year old.

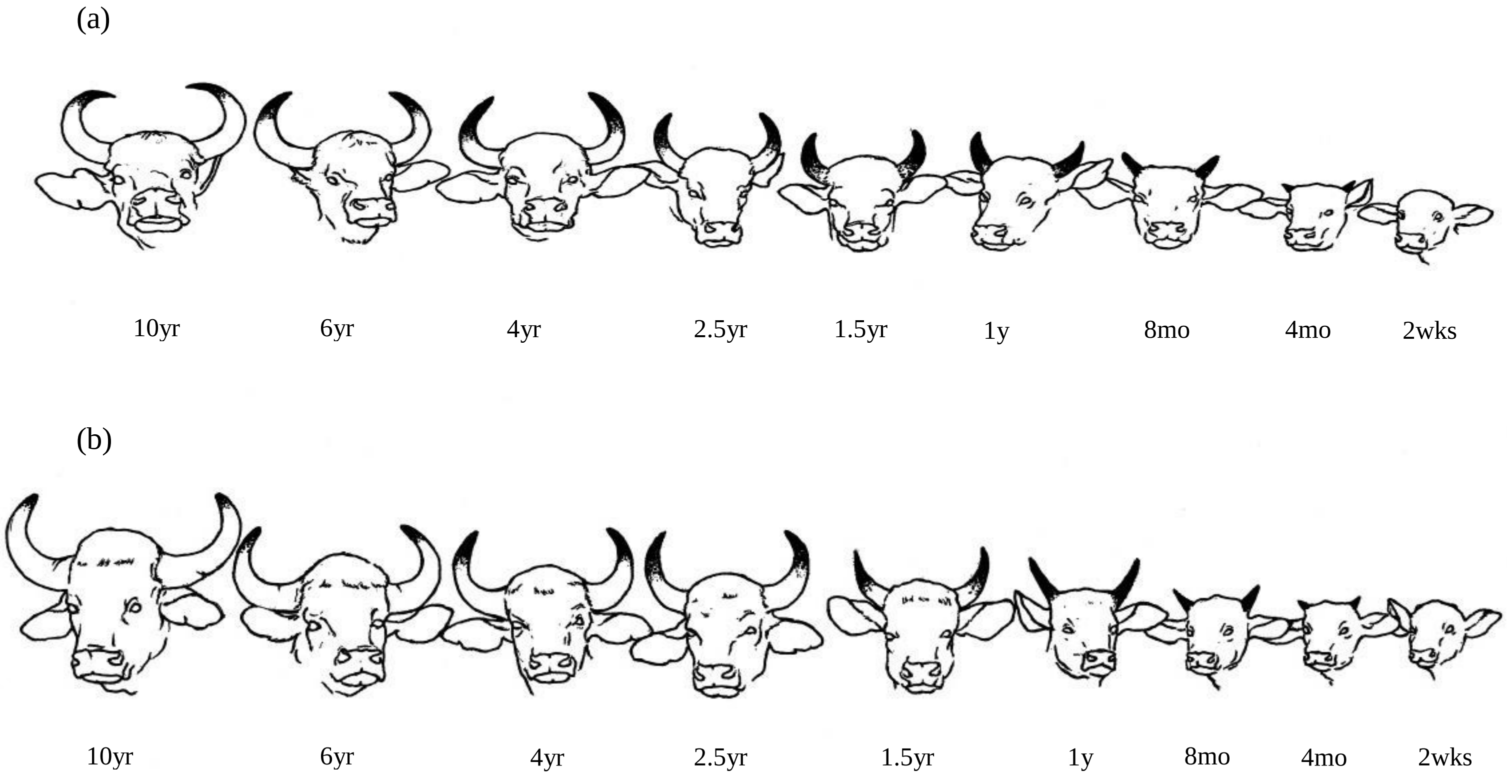


Fig. 5.3. Relative age-specific differences of (a) female and (b) male gaur *Bos gaurus* head and horns drawn from photographs of individuals of known age.

6

First detailed analysis of life history traits of the Asian megaherbivore, gaur *Bos gaurus*

Farshid S. Ahrestani, Subramaniam Iyer, Ignas M.A. Heitkönig and Herbert H.T. Prins

Abstract

Large ungulate *life history* is characterized by high longevity, low recruitment, low calf survival, and high adult survival that is often female-biased. The *life history* of some Bovini tribe species like the African buffalo and the American and European bison are well understood. This, however, is the first analysis of *life history* traits of Asia's largest Bovini species, the gaur. Data were collected from a 20 month long (December 2005 to August 2007) field-based study in Bandipur and Mudumalai Tiger Reserves, South India, supplemented by data from both the world's and India's largest captive gaur populations. Female gaur begin to recruit at the age of three years and apparently remain fertile even in old age. Their 9-10 month gestation period enables female gaur to give birth every 390 days in captivity. Adult females dominate gaur populations; this study found adult females three times more abundant than adult males. Survival of male gaur is probably lower than that of females beyond the age of three years, the age beyond which sexual dimorphism becomes prominent and male gaur begin their solitary lives. Mortality of calves under captive conditions was found to be high, and a low calf:female ratio found in the field suggests that calf mortality is high for gaur in the wild too. Maximum longevity of both sexes of gaur has not exceeded 24 years in captivity; 20-25 years is the estimated longevity of gaur in the wild. In conclusion, gaur exhibit *life history* characteristics of the slow pattern true to their large body mass and similar to other similar-sized phylogenetically related Bovini species.

Introduction

Large herbivores exhibit *life history* traits of the slow pattern: recruitment is low, maturity occurs late, and generation times and life-spans are long (Stearns, 1992; Oli, 2004). In addition, survival in large herbivores is low in the pre-weaning stage, high in the prime adult stage, and decreases in old age (Caughley, 1966; Spinage, 1972). Also in large herbivore populations, adult females often have higher survival rates than adult males (Berger & Gompper, 1999; Toïgo & Gaillard, 2003).

As a function of their large body mass and *life history* traits, population growth of large herbivore species is low (Millar & Zammuto, 1983; Calder, 1996; Oli & Dobson, 2003) and is generally controlled in varying degrees by forage availability, predation, and diseases (Sinclair, 1989; Saether, 1997). Predation effects on large herbivore individuals of different age and sex can vary both spatially and temporally (Mills & Shenk, 1992; Prins, 1996). While some large ungulate populations are affected by diseases continually (Joly & Messier, 2004; Cross & Getz, 2006), others are impacted by episodic disease outbreaks, sometimes of epidemic proportions (Sinclair, 1977; Prins & Weyerhaeuser, 1987; Choudhury, 2002). In general, population growth of large herbivores is more sensitive to adult than juvenile survival, and is less sensitive to fertility (Gaillard *et al*., 2000).

Studies of Bovini tribe (Family: Bovidae, Sub-Family: Bovinae) species like the banteng *Bos javanicus* (Hoogerwerf, 1970; Choquenot, 1993), African buffalo *Syncerus caffer* (Grimsdell, 1969; Sinclair, 1977; Prins, 1996; Jolles, 2007), North American bison *Bison bison* (McHugh, 1958; Fuller, 1961; Vuren & Bray, 1986), and European bison *Bison bonasus* (Krasinska & Krasinski, 2007) have shown that these species exhibit *life history* characteristics of the slow pattern (Stearns, 1992; Oli, 2004). There exists, however, little understanding of the *life history* and demography of Asia's largest Bovini species, gaur *Bos gaurus*. Since the opportunistic observations and the interpretations thereof made by Schaller (1967), scant information has been added to the literature regarding gaur for more than 40 years.

Therefore, to update understanding of the fundamental biology of a poorly understood and threatened species—based on a 20 month field study of a wild gaur population in South India from December 2005 to August 2007, supplemented with data from the world's largest captive gaur population housed in Henry Doorly Zoo, USA, and India's largest captive population housed in Mysore Zoo, South India—we present the first analysis of gaur *life history* traits in the context of its predicted slow *life history* as a function of its large body mass. *Life history* traits correlate to body size (Peters, 1983; Schmidt-Nielsen, 1984; Calder, 1996); allometric scaling of *life history* traits is documented even within the large mammalian herbivore guild (Western, 1979). Furthermore, phylogenetically related species exhibit similar life-history traits (Fairbairn, 1997). Therefore, l*ife history* traits of gaur would be expected to be similar to that of other similar body sized Bovini species. So to enable making better inferences from our data, we restricted comparing data of gaur with that of other Bovini species for which data were available, like the banteng, African buffalo, and American and European bison.

Methods

Reproductive traits and longevity

Data of captive gaur were compiled from: 1) all (*n* = 41) gaur that were part of India's largest captive gaur population housed at Mysore Zoo, India, from 1994 to 2006; and 2) all (*n* = 130) gaur that lived their entire lives between 1968 and 2006 with what is now the world's largest captive gaur population at Henry Doorly Zoo, Omaha, NE, USA. The combined zoo data were used to derive sex ratio at birth and longevity of both sexes. Since mating was controlled by staff in Omaha Zoo, reproductive traits such as age at first reproduction and inter-birth interval were estimated using only the Mysore Zoo data.

Age-sex structure and survival

To determine gaur population structure by age and sex, two contiguous Tiger Reserves in South India—Mudumalai (329 km^2; N $11^{o}32^{'}$-$43^{'}$, E $76^{0}22^{'}$-$45^{'}$) and Bandipur (880 km^2; N $11^{o}36$-$57^{'}$, E $76^{o}13$-$52^{'}$)—were surveyed for gaur between January 2006 and August 2007. Most data were collected from a 200 km^2 study area (Fig. 1.1) that was split equally between the two Reserves; a distance of less than 4 km separated the areas sampled in each park. Given the difficulty in observing gaur in forested areas, and the fact that gaur were more tolerant of humans in vehicles than on foot, the majority of data were collected using an open-topped jeep while systematically sampling the study area along its 50 km road network. The sampling effort for the study period exceeded 3750 km and was restricted mainly to dawn and dusk, times when gaur were both active and visible.

Gaur were classified into three unsexed age-classes below the age of one year, and four age classes for females and five for males above the age of one year (Table 6.1). Classification of individual gaur by sex and age were done using methods described by (Chapter 5). Often individuals were classified based on the shape, size, and the amount of white of their horns. While it was relatively easy to differentiate between the sexes of adult gaur, sexing individuals in the age group of 1-2 years proved challenging. A total of 1620 observed gaur were classified during the study. Admittedly, the sampling included pseudo-replication (Hurlbert, 1984), an issue any study of this nature would encounter. Since this was not a controlled experimental based study it was difficult to correct for pseudo-replication. However, we feel—given the large sample size obtained, the wide range of habitats sampled, and knowing that different herds were sampled based on a comparison of photographs of animals sampled—that the data obtained provided a valid picture of the age-sex ratio of the gaur population in the study area.

Table 6.1. Age classes that individuals were assigned to while sampling gaur population in Mudumalai and Bandipur National Parks, India, based on morphological differences.

Calves			Males					Females			
C1	C2	C3	M1	M2	M3	M4	M5	F1	F2	F3	F4
0-2 mo	3-5 Mo	6-12 mo	1-2 yr	2-3 yr	3-5 yr	5-8 yr	>8 yr	1-2 yr	2-3 yr	3-10 yr	>10 yr

Since information on sex ratio at birth from captive populations of gaur remained inconclusive (this study), reference was made to studies of other Bovini species that showed sex ratio at birth did not differ significantly from parity: African buffalo, 1.00 (Grimsdell, 1969; Sinclair, 1977; Prins, 1996); American bison, 1.00 (Green & Rothstein, 1991; Fuller *et al.*, 2007); European bison, 0.98-1.00 (Mysterud *et al.*, 2007; Krasinska & Krasinski, 2007); and banteng, 1.00 (Hoogerwerf, 1970; Choquenot, 1993). The lack of any size-based sexual dimorphism between the sexes in the first year, led us to assume that survival for both sexes of gaur through the first year is the same in the wild. Therefore, numbers of wild male and female gaur in the first year were calculated as half the number of gaur found in the age class 0-1 year.

As a standardized age classification system was not used by previous gaur population studies, data from these earlier studies were compared to data from this study by grouping population structure data into gaur calves (C; <1 year):adult males (AM; >1 year):adult females (AF; >1 year).

Data of age at death of 72 male and 58 female gaur from Omaha Zoo (1968-2006) were used to construct a life table and to compare survival between both sexes. We also fitted standard survival functions to the field data while assuming that the sampled gaur population had a stationary age distribution with constant fertility and mortality (Caughley, 1966). The survival functions fitted to our data were: 1) the exponential function, the simplest function that describes the steadily decreasing $l(x)$ series (Aitkin & Clayton, 1980),

$$l(x) = l(0)\exp(-\alpha x) \qquad (1)$$

The exponential function, however, reaches zero only at infinity and results in a constant rate of mortality (determined by α) for all ages. As both these constraints make the exponential function a bit unrealistic, we developed, 2) a modified exponential function that generated an increasing rate of mortality (determined by α) and accounted for maximum life span ω, that we assumed to be 25 years for both sexes,

$$l(x) = l(0)\frac{\exp(-\alpha x) - \exp(-\alpha\omega)}{1 - \exp(-\alpha\omega)} \qquad (2)$$

The modified exponential function was fitted to the data by the non-linear least squares method. Finally, 3) the two-parameter Weibull function was also fitted to our data (Pinder, Wiener & Smith, 1978),

$$l(x) = l(0)\exp\left(-\left(\frac{x}{b}\right)^{c}\right) \qquad (3)$$

where the shape c and scaling b parameters were estimated applying the linear least squares method to the data converted into logarithmic scales.

Results

Reproduction and life-span

In Mysore Zoo the mean age at first reproduction for females was 37.6 months ($n = 5$). The mean inter-birth interval of seven births for three young females (< 6 years) was 398 days, and the oldest female in Mysore, who lived to about 18 years, reproduced 14 times during her lifetime with a mean inter-birth interval of 373 days.

The ratio of males:females at birth varied between 0.86 ($n = 41$) in Mysore Zoo to 1.36 ($n = 180$) in Omaha Zoo. Records from Omaha Zoo showed that the longevity for females was greater than that of males: 17% of females ($n = 58$) lived beyond 15 years, the oldest reaching the age 22.5 years; only one male ($n = 72$) lived beyond 15 years, but this male lived the longest (23.6 years) of all 130 individuals sampled.

Age-sex structure

Adult females dominated (50.3%) the sampled free-ranging gaur population and were three times more abundant than adult males (Figs. 6.1, 6.2). This female-biased trend was consistent across three consecutive six-month periods of the study: (male:female = 26.1:73.9) January-June 2006, (26.2:73.8) July-December 2006, (24.4:75.6) January-June 2007, respectively. The female-biased adult sex ratio found in this study was similar to what other studies of gaur in India have shown (Fig. 6.3), and is similar to ratios reported in studies of other Bovini species (Table 6.2).

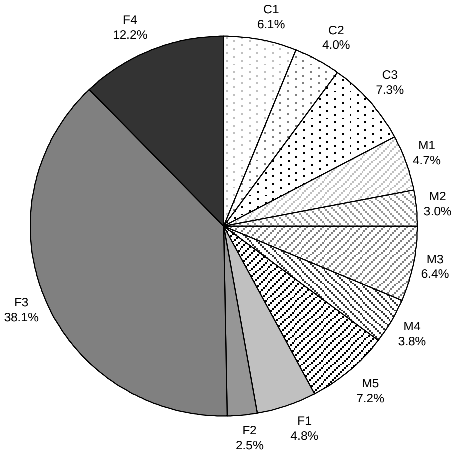


Fig. 6.1. Structure of gaur population found in contiguous Mudumalai and Bandipur National Parks, South India, between January 2006-August 2007. Age-sex classes: C1=calves 0-2 months; C2= calves 3-5 months; C3= calves 6-12 months; M1=males 1-2yrs; M2=males 2-3yrs; M3=males 3-5yrs; M4=males 5-8yrs; M5= males >8yrs; F1=females 1-2yrs; F2=females 2-3yrs; F3=females 3-10yrs; F4=females 10yrs.

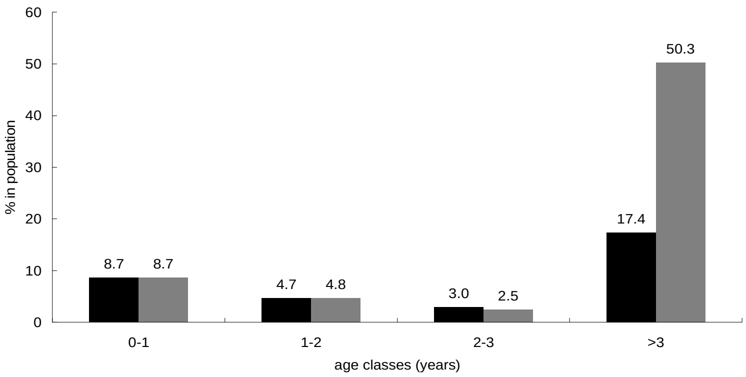


Fig. 6.2. Percentages of male and female gaur in four age classes. (Mudumalai and Bandipur National Parks, South India, January 2006-August 2007).

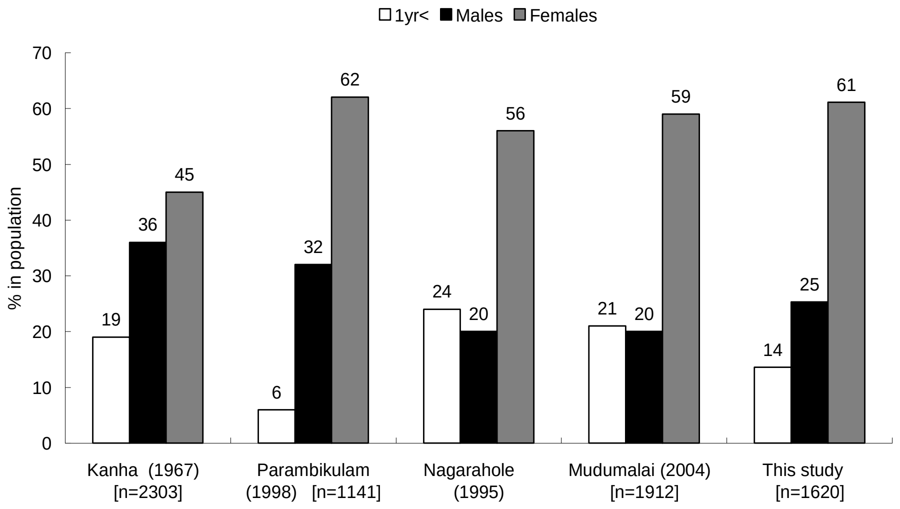


Fig. 6.3. Percentage distribution of calves (<1yr), males (>1yr), and females (>1yr) found in the field study in comparison with four other gaur studies in India. Literature sources are: for Kanha National Park, Madhya Pradesh - Schaller (1967); for Parambikulam Wildlife Sanctuary, Kerala - Vairavel (1998); for Nagarahole National Park, Karnataka - Karanth & Sunquist (1995); for Mudumalai National Park, Tamil Nadu - Kumar *et al.* (2004); This study: Mudumalai & Bandipur National Parks, South India.

Table 6.2. Male:female ratio of adults of different populations of three large Bovid species: banteng *Bos javanicus*, feral cattle *Bos taurus*, American bison *Bison bison*, European bison *Bison bonasus*, and African buffalo *Syncerus caffer*.

Species	Population	Ratio M:F	References
Bos javanicus	Udjung Kulon, Indonesia	0.32	Hoogerwerf, 1970
Bos Taurus (feral)	Amsterdam Isle, Indian Ocean	0.61	Berteaux, 1993
Bison bison	Henry Mountains, USA	0.56	Vuren & Bray, 1986
	Badlands, USA	0.81	Berger & Cunningham, 1994
	Mackenzie, NWT, Canada	0.84	Gates *et al.*, 1991
Bison bonasus	Bialowieskiej, Poland	0.68	Krasinska & Krasinski, 2007
Syncerus caffer	Lake Manyara, Tanzania	0.22	Prins & Iason, 1989
	Kainji Lake, Nigeria	0.43	Aremu *et al.*, 2007
	Serengeti, Tanzania	0.63	Sinclair, 1977

Survival

The percentages of free-ranging gaur in the first three single-year age classes were low and showed a decreasing trend with increasing age for both males and females: males decreased 8.7(estimated) > 4.7 > 3.0 and females decreased 8.7(estimated) > 4.8 > 2.5 (Fig. 6.2). Analysis of the captive gaur data from Omaha Zoo, showed that females have higher survival than male gaur through much of their lifespan (Appendix 6.1).

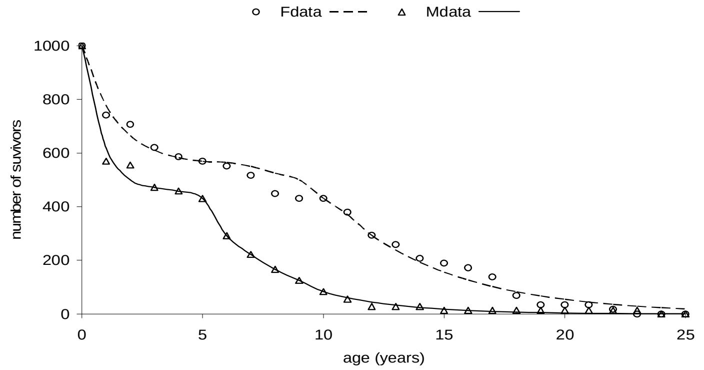


Fig. 6.4. Survival curves fitted to data of age at death for female (n = 58) and male (n = 72) gaur that were part of what is now the world's largest captive gaur population at Henry Doorly Zoo, Omaha, NE, USA, 1968-2006.

The parameter α estimated while fitting the exponential function to our data was 0.17 for males and 0.11 for females. Assuming the maximum life span to be 25 years for both males and females, the parameter α of the modified exponential function was found to be 0.42 for males and 0.26 for females. With respect to the Weibull function, b and c were estimated as 2.91 and 0.65 for males and 5.15 and 0.37 for females, respectively. To compare the fits of the three curves to the data (Figs. 6.5a,b), the sum of squares of the deviations (SSD) of function estimates from observed data was calculated. For males, SSD of the modified exponential function was 916, which was lower than the SSD of 1727 and 5861 of the Weibull and exponential functions, respectively. For females, the 6042 SSD of the Weibull function was the lowest, and SSD for the modified exponential and exponential functions were 6431 and 7872, respectively.

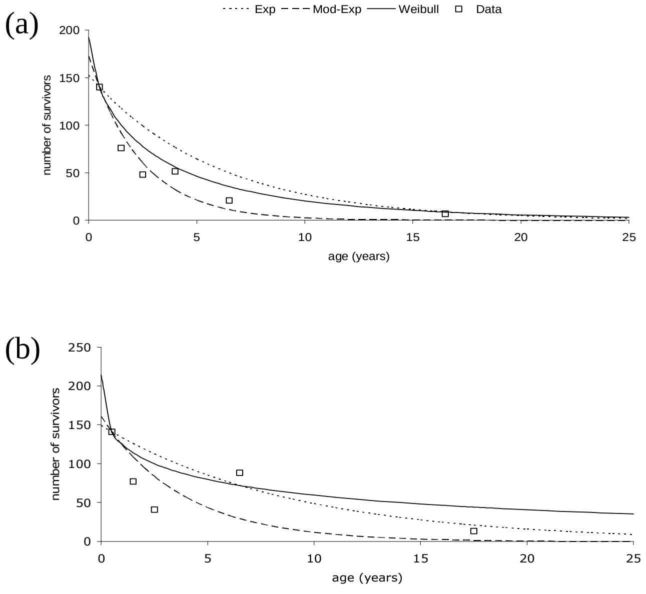


Fig. 6.5. An exponential (Exp) function, a modified exponential function (Mod-Exp), and the Weibull distribution fitted to survival data of (a) male, and (b) female gaur found in Mudumalai and Bandipur National Parks, India, from January 2006 to August 2007.

Discussion

Reproduction

Age at first conception (primiparity) was found to be three years for captive gaur (Mysore Zoo, this study). This data does not confirm whether free-ranging female gaur begin to recruit at the age of three, but it can be relied upon for suggesting that female gaur become sexually mature at around 26 months. Data from free-ranging populations of other Bovini species like the banteng, American and European bison (Table 6.3) show that three years is the average primiparity in these species. Although ovulation in African buffalo can begin as early as 18 months, they have been observed to calve only at 4-5 years in the wild (Table 6.3), making them the Bovini species that begin recruitment at the oldest age. Combining the data regarding captive gaur (this study), and given that three years is the minimum age of primiparity of other Bovini species, suggests that three years is the minimum primiparity for wild female gaur too.

Although gaur females begin recruiting late, it appears that they also remain fertile in old age. This is based on personal observations of old female gaur accompanied by calves in the wild, in addition to the fact that an 18 year old female in Mysore zoo gave birth to her fourteenth calf a few months before her death. Old aged females of other Bovini species (Table 6.3) have also been observed to calve; in fact there exists one record of North American bison females over the age of 40 years found accompanied by calves (McHugh, 1958).

Table 6.3. Life history traits of gaur Bos gaurus compared to that of other Bovini species.
Note: Numbers alongside data denote source.

Species	*Primiparity*	*Oldest age at conception (years)*	*Calf:100 adult females*	*Maximum Longevity*
Bos gaurus	3 years [1]	18 [1]	34:100 [1] 35:100 [9]	F : 24 years [1] M : 23.6 years [13]
Bos javanicus	3 years [2]	24 [2]	23:100 [2]	20-25 [2]
Bison bison	92% pregnant at 3 years [3] 82% pregnant at 3	40+ [3]	62:100 [10] 76:100 [11]	F : 40+ years [3] M : 20+ years [3]
Bison bonasus	3-4 years [5]	24 [5]	48:100 [5]	F : 23-27 years [5] M : 20-22 years [5]
Syncerus caffer	4 years [6,7,8]	16 [7]	70:100 [6] 74:100 [12]	23-25 years [6,8,14]

Sources: [1] = This study; [2] = Hoogerwerf (1970); [3] = McHugh (1958); [4] = Green & Rothstein (1991); [5] = Krasinska & Krasinski (2007); [6] = Sinclair (1977); [7] = Grimsdell (1969); [8] = Prins (1996); [9] = Schaller (1967); [10] = Vuren & Bray (1986); [11] = Bradley & Wilmshurst (2005); [12] = Jolles (2007); [13] = Crandall (1964); [14] = Spinage (1972).

Data from Mysore Zoo showed that captive female gaur are capable of one birth a year. This is not surprising as gestation period for gaur is of 9-10 months (personal communications: Joe Sheppard, Omaha Zoo, USA & Dr. Nanjappa, Mysore Zoo, India; Hubback, 1937; Schaller, 1967). The calving interval between successive gaur births can be calculated from ‘gestation time / fertility rate’ (Sinclair, 1977). This give us an estimate of 828 days when fertility rate = 0.35 (derived from the calf:female ratio found in this study), but 386 days when fertility rate = 0.75 (which was the rate found for captive gaur in Mysore Zoo; was the fertility rate estimate that Schaller (1967) made in his study; and is also the average fertility rate reported by Sinclair (1977) for African buffalo). The estimate of 386 days is similar to the inter-birth interval estimate of 52-54 weeks for North American bison (Green & Rothstein, 1991) and the 1-2 years inter-birth interval found for African buffalo (Grimsdell, 1969; Prins, 1996) and European bison (Krasinska & Krasinski, 2007). It is not possible to come to any conclusion about the average inter-birth interval of female gaur in the wild. Considering, however, the higher estimate of the two years inter-birth interval found for other wild Bovini species, gaur females reaching the age of 20 years can be expected to produce 8-10 calves in their lifetime.

Survival

Adults

The higher percentage of females in adult gaur populations is similar to what has been found for many other large herbivore species (Berger & Gompper, 1999). Although the probability of detecting solitary animals, usually adult male gaur, might have been less than that of detecting a herd mainly composed of adult females, we are confident that adult gaur sex ratio in our field study is in fact female biased. This confidence stems from the understanding that 1) despite their solitary nature, the probability of detecting adult males in the field was high because of their large size and their indifference to human presence; 2) all four other studies of wild gaur populations in India show a similar result (Fig. 6.3); and 3) female-biased adult sex ratios have been reported from all studies of other Bovini species (Table 6.2).

Berger and Gompper (1999) found that in most extant ungulate populations males died disproportionately to their abundance and they concluded that this was a direct consequence of greater age-specific mortality in males. Results from fitting survival curves to our field data showed that the rate of mortality (determined by α; see Methods) was higher for males than that of females for both the exponential and modified exponential functions, indicating a higher mortality for males than for females. In addition, Karanth and Sunquist (1995) found that in Nagarahole National Park, South India, adult female and adult male gaur comprised, respectively, 22.6% and 14.6% of all tiger *Panthera tigris* kills, a ratio of 1.5:1. These mortality data were reported along with a 56:20 adult female:adult male ratio, i.e. 3:1. The comparison between the live adult and the kills ratios suggests that mortality due to predation is higher among adult male than female gaur.

As to why male gaur mortality is higher than females, a recent long-term study of buffalo in Kruger National Park, South Africa, (Hay *et al*., 2008) found that the greater predation of male buffalo by lions was a function of male buffalo willing to trade increased predation risk for additional energy gains to increase their reproductive success. This is similar to the conclusions that Clutton-Brock *et al*. (1982) and Prins and Iason (1989) reached, i.e., that higher mortality of adult males in large herbivore populations was a result of the increased time and energy invested by males in reproductive behaviour. In addition, the increased energy requirements of greater growth rate and longer growth period in males has also been recognized to predispose males to a greater number of mortality factors than females (Prins, 1996; Berger & Gompper, 1999). It is worth noting that data from Omaha Zoo showed that in captivity too—where the species is free from predation—male gaur had lower survival than females. This finding is further supported by the comprehensive review of Kohler *et al*. (2006) of captive animal populations that found female hoof stock survival higher than males by 38%. While injuries sustained during fights between males that cause death directly, or expose males to other mortality causes, are also understood to contribute to higher mortality of males than females in large herbivores (Geist, 1986), this is probably not the case with gaur. Adult male gaur rarely engage in fights (Schaller, 1967; Personal observations), a trait that is also shared by other Bovini tribe species (banteng: Hoogerwerf, 1970; African buffalo: Prins, 1996; European bison: Krasinska & Krasinski , 2007).

Therefore, based on current hypotheses that explain female-biased adult sex ratios in large herbivores—and supported by the facts that adult male gaur live much of their adult lives solitarily and that sexual size dimorphism is high in adult gaur—it appears reasonable to assume that survival of adult gaur males is lower than that of adult females and is probably a consequence of a greater investment by males than females into increasing their fitness. Although adult male gaur have lower survival than adult females, the survival of male gaur (5-8 years) is probably high in absolute terms, as reported for all other Bovini species (Hoogerwerf, 1970; Sinclair, 1977; Berger & Cunningham, 1994; Prins, 1996; Krasinska & Krasinski, 2007).

Regarding when survival of male gaur becomes lower that that of females, it likely is beyond the age of 3 years. Three years is the age above which sexual size dimorphism in gaur becomes noticeable (Chapter 5) and is also the age at which males normally begin their solitary lives (personal observations); before this time males remain within herds. The field data also suggests that there is little difference in survival between the sexes till the age of three years (Fig. 6.3). Furthermore, studies of other Bovini species have also reported similar results, for example survival rates of male African buffalo have been found to be lower than females only after the age of 3-4 years (Grimsdell, 1969; Sinclair, 1977).

A review of the literature of diets of the three major predators that overlap in range with gaur, the tiger, leopard *Pathera pardus,* and dhole *Cuon alpinus* (Johnsingh, 1992; Karanth & Sunquist, 1995; Venkataram *et al*., 1995; Ramakrishnan *et al*., 1999; Andheria *et al*., 2007) indicates that tiger predation seems to play a role in gaur mortality: tiger diet consists of 8-24% of gaur, leopards include less than 3%, and dhole less than 2%, of gaur in their diet. Karanth and Sunquist (1995) also showed that young (<1 year) gaur made up nearly 60%, 88%, and 100% of tiger, leopard, and dhole gaur kills recorded, respectively.

Calves

Mortality of African buffalo calves has been found to be as high as 50% (Sinclair, 1977), mortality of banteng in the first six months has been reported to be 26% (Choquenot, 1993), and mortality of gaur calves in Omaha Zoo was found to be 36% (this study). These data suggest that calf mortality is likely to be high in wild gaur populations too. This explains why studies, including ours, found low estimates of calf:female ratios (Table 6.3). There exists, however another reason for the low calf:female ratios observed in field surveys of gaur so far, which is the underestimation of young calves during surveys. It is likely that gaur calves below the age of two months are missed during surveys: 1) because of their small size, 2) their light brown coloration that blends in well with the undergrowth, and 3) their habit of sitting concealed in undergrowth in the first few months of their lives (Hubback, 1937).

Longevity

With respect to longevity, the maximum age recorded for both sexes of gaur in captivity has not exceeded 24 years. This is similar to estimates of the Bovini species, although American bison females have been found alive, and with calves, at over 40 years (Table 6.3). Therefore, while some individuals might live to older ages, there is little reason not to believe that 20-25 years is the maximum longevity of gaur in the wild.

Conclusions

Gaur, in accordance to its large body mass, exhibits *life history* characteristics of the slow pattern similar to other Bovini species: females begin to recruit for gaur populations only after the age of 3 years, though they remain fertile in old age; recruitment appears to be low; survival of adult female gaur appears to be higher than adult males, which probably begins beyond the age of three; juvenile survival appears to be low, irrespective of sex; and finally gaur are long-lived species, reaching an apparent maximum age of 20-25 years.

There is a need for further studies—that ideally include monitoring animals of known ages in the wild—to make better estimates of age-specific vital rates of this vulnerable species.

Appendix 6.1. Life table for gaur *Bos gaurus*. Source: Captive population data from Omaha Zoo. *l(x)* = number of individuals surviving to age *x* (years). *l'(x)* = *l(x)* transformed to an initial population of 1000 individuals.

Age	*l(x)* males	*l'(x)* males	*l(x)* females	*l'(x)* females
0	72	1000	58	1000
1	41	569	43	741
2	40	556	41	707
3	34	472	36	621
4	33	458	34	586
5	31	431	33	569
6	21	292	32	552
7	16	222	30	517
8	12	167	26	448
9	9	125	25	431
10	6	83	25	431
11	4	56	22	379
12	2	28	17	293
13	2	28	15	259
14	2	28	12	207
15	1	14	11	190
16	1	14	10	172
17	1	14	8	138
18	1	14	4	69
19	1	14	2	34
20	1	14	2	34
21	1	14	2	34
22	1	14	1	17
23	1	14	0	0
24	0	0	0	0
25	0	0	0	0

7

Determinants of large herbivore diversity in sub-Himalayan India

Farshid S. Ahrestani, Ignas M.A. Heitkönig, Frank van Langevelde, V. Srinivas, M.D. Madhusudan and Herbert H.T. Prins

Abstract

The goal of this study was to test whether the relationships between plant available moisture (PAM), plant available nutrients (PAN), and body mass explain the distribution of diversity of large herbivores in Sub-Himalayan mainland India. Specifically, we tested whether the frequency of occurrence of larger herbivores increases with increasing PAM, but is relatively independent of PAN; and the frequency of occurrence of smaller herbivores decreases with increasing PAM, but increases with increasing PAN. The occurrence of 16 large herbivore species in 77 Indian Protected Areas south of the Himalayas were analyzed with respect to PAM and PAN. PAM was calculated as ^{10}log(rainfall/potential evapotranspiration) while cation exchange capacity was used for PAN. We analyzed herbivore species diversity, the average body mass of herbivore species, and their frequency of occurrence in relation to PAM and PAN using ANOVA, correlation, regression and correspondence analysis. Herbivore species diversity was highest at levels of high PAN and intermediate PAM. PAM emerged as a strong predictor of large herbivore species diversity in India. Mean body mass of all species in an area increased with increasing PAM but decreased with increasing PAN. The frequency of occurrence of the largest species like Asian elephant *Elephas maximus* and gaur *Bos gaurus* increased with increasing PAM. The opposite was true for the smallest species, the chinkara *Gazella bennettii*, as its frequency of occurrence decreased with increasing PAM and it was absent from the wettest areas. Patterns were reversed, however, with respect to PAN: frequency of occurrence of the Asian elephant decreased with increasing PAN, while that of the chinkara increased. Areas with the highest levels of PAN and intermediate levels of PAM support the highest herbivore species diversity and mean body mass of all herbivores. This study contributes to understanding patterns in herbivore species diversity in relation to PAM and PAN.

Introduction

Understanding patterns in species diversity has been an important theme in ecological research (Rosenzweig, 1995; Olff *et al*., 2002). Studies that have specifically investigated patterns of large herbivore species diversity have focused their attention on Africa (Du Toit & Cumming, 1999; Andrews & O'Brien, 2000), where large herbivore species richness is the highest in the world (Dorst & Dandelot, 1970). Many of these African-based studies found that spatial variation in large herbivore biomass and diversity (defined in this paper as species richness, cf. Olff *et al*. (2002)) correlated significantly to the distribution and heterogeneity of forage resources (Coe *et al*., 1976; East, 1984; Du Toit & Owen-Smith, 1989; Fritz & Duncan, 1994). Studies have also proposed theoretical models capable of predicting the distribution of large herbivore diversity (McNaughton *et al*., 1988; Prins & Olff, 1998). Most studies concluded that diversity of large herbivore species in an area is defined by a complex set of interactions between environmental variables, herbivores, and plants.

Olff *et al*. (2002), however, developed a simple theoretical framework that predicts large herbivore diversity on a global scale based on only two environmental variables, namely plant available moisture (PAM) and plant available nutrients (PAN). Although other abiotic and biotic variables also influence primary production (McNaughton, 1985; Collins *et al*., 1998; Thuiller *et al*., 2004), PAM and PAN are considered the two most important determinants of plant quantity and quality (Milchunas *et al*., 1995). Quantity (defined here as biomass density) and quality (defined here as nutrient concentrations) of primary production, however, vary differently along PAM and PAN gradients: quantity is positively related to both PAM and PAN, while quality is positively related to PAN and negatively related to PAM (Milchunas *et al*., 1994; Walker & Langridge, 1997).

The model of Olff *et al*. (2002) also included two principles that relate body mass and resource consumption by herbivores: (1) large-bodied herbivores, because of their lower metabolic requirements per unit body mass and higher gut retention times, can survive on resources of lower quality than can small-bodied species; and (2) small-bodied herbivores, because of their lower absolute metabolic requirements, can survive in areas where low plant biomass production cannot support large-bodied herbivores (Kleiber, 1932; Bell, 1971; Jarman, 1973; Demment & Van Soest, 1985; Owen-Smith, 1988). Herbivore species of different body mass would thus persist within 'resource wedges' delimited by different levels of plant quantity and quality thresholds (Olff *et al*., 2002). Since PAM and PAN determine the variation in plant quantity and quality, it follows that PAM and PAN levels in an area would determine the diversity of herbivore species that could persist in a given area.

Olff *et al*. (2002) validated their predictions by analyzing data related to North America and sub-Saharan Africa. They also made predictions of diversity patterns for Asia, which remain untested. We believe that within Asia, sub-Himalayan India is adequately large (2,500,000 km^2 land cover), has sufficient variation in moisture and soil nutrients, and a rich enough large herbivore assemblage to validate these predictions. The main goals of this study were to investigate whether in sub-Himalayan India (1) large herbivore species diversity and their mean body mass in India could be explained by PAM and PAN; and (2) distribution patterns of mammalian herbivore species validate the following body mass based predictions: a) the frequency of occurrence of larger herbivores increases with increasing PAM, but is relatively independent of PAN; and b) the frequency of occurrence of smaller herbivores decreases with increasing PAM, but increases with increasing PAN.

Methods

Data collection

The combined extent of six of India's nine mainland biogeographic zones defined our study area: Indian Desert, Semi-Arid, Western Ghats, Deccan Peninsula, Gangetic Plain, and the North East (Rogers & Panwar, 1988). The Western Ghats and North East zones are characterized by high rainfall and high biodiversity. The Deccan Peninsula is the largest zone, encompassing the Deccan plateau, and is characterized by volcanic soils and distinct wet and dry seasons. The Gangetic Plain encompasses the flood plain of the river Ganges.

Following Olff *et al.* (2002), we restricted our analyses to large herbivore species with mass > 2kg. Our data set included occurrence of 16 large herbivores species from 77 protected areas in India (Fig. 7.1, Table 1.1, Appendix 7.1). We selected protected areas > 200km^2 to decrease the probability of selecting small areas that might have experienced recent extirpations, particularly of the largest species. Geographic locations of the 77 protected areas were based on UNEP's World Database on Protected Areas and the presence/absence of the 16 herbivore species in each protected area were verified by leading Indian wildlife experts (A.J.T. Johnsingh & J.C. Daniel, personal communications).

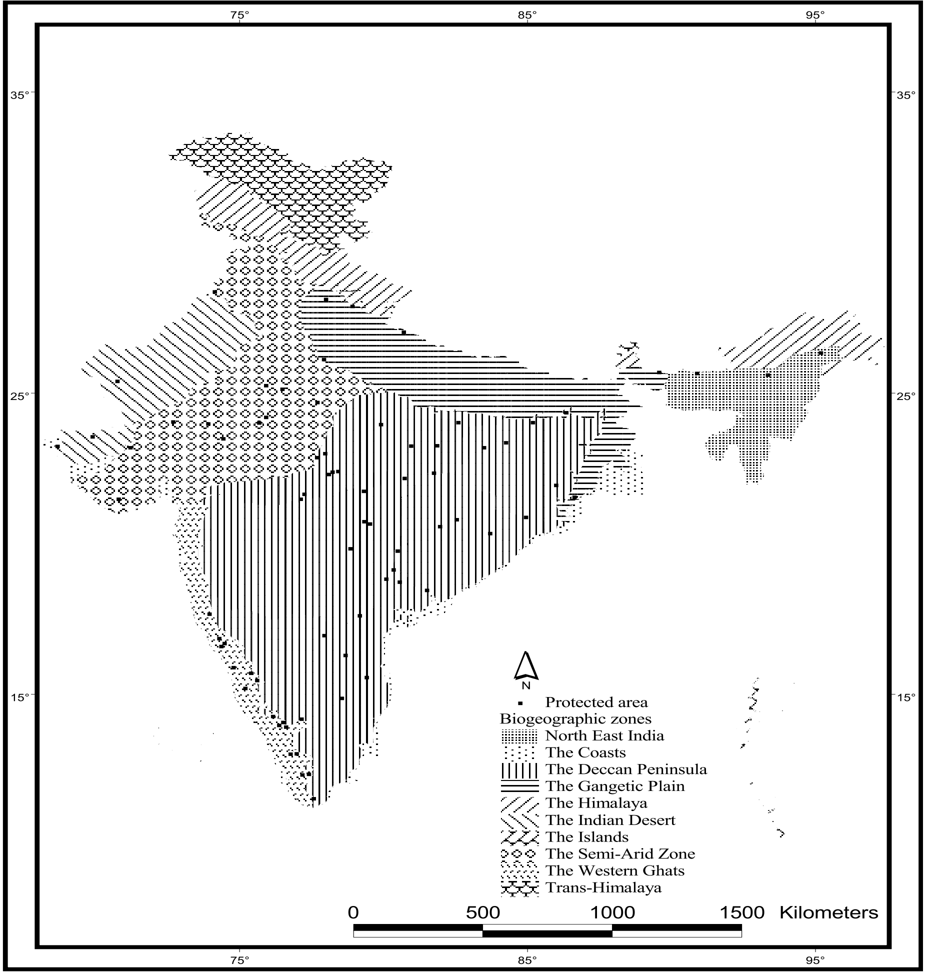


Fig. 7.1. India's biogeographic zones and the location of 77 protected areas chosen for analyzing large mammalian herbivore species diversity in sub-Himalayan India (Rogers & Panwar, 1988).

PAM for each protected area was calculated as ^{10}log(annual rainfall/annual potential evapotranspiration) (Olff *et al*., 2002). Rainfall data were derived from Hijmans *et al*.'s (2005) WorldClim database at a spatial resolution 0.5 x 0.5 arc minutes (1km is approximately 0.5 arc minutes), and potential evapotranspiration from Ahn & Tateishi (1994) at a spatial grid cell resolution of 30 x 30 arc minutes (Fig. 7.2a). Estimates of PAN were derived at a scale of 5 x 5 arc minutes from ISRIC's global soil database (Batjes, 2006). At a scale of 5 x 5 arc minutes, the ISRIC database provides data for total nitrogen (g kg^{-1}), organic carbon content (g C kg^{-1}), and cation exchange capacity (cmol$_c$ kg^{-1}), but not for phosphorus. To enable a comparison with predictions made by Olff *et al*. (2002) we used cation exchange capacity of the top 20cm of soil as an index of PAN (Mengel & Krikby, 2001; Fig. 7.2b). The PAM index for our sites ranged from –0.84 to 0.52 and the PAN index ranged from 3.2 to 42.5. Since the datasets of PAM and PAN were of different spatial resolutions, their values were derived from a single point location for each site rather than from an averaged value of the polygons of protected areas.

Statistical analysis

Correlation analysis and ordinary least squares (OLS) multiple regression were used to evaluate species diversity as a function of PAM and PAN across sites. In the OLS, we also included possible quadratic effects of PAM and PAN. Since the data were spatial in nature, we repeated the multiple regression analysis using simultaneous autoregression (SAR) models that correct for potential spatial auto-correlation biases in datasets (Kissling & Carl, 2008). We used the software program Spatial Analysis in Macroecology (Rangel *et al*., 2006) to analyze our data using SAR models but found that autoregression analyses results were similar to results from using OLS models, suggesting that spatial autocorrelation was not an issue with our data.

To test the body mass-based predictions, the mean body mass of all large herbivore species present in a protected area (MBM) were graphed in different intervals of indices of PAM and PAN and analyzed using an ANOVA. To test whether the presence of the largest herbivore species, the elephant, had an effect on mean body mass, we included elephant as a binary factor in the OLS multiple regression. In addition, the frequency of the occurrence of five species were compared in relation to PAM and PAN. Body mass range of the five selected species spanned 17-3120 kg, and the species included were the smallest (chinkara *Gazella bennetti*), the largest (Asian elephant *Elephas maximus*), and three species with weights in between (chital *Axis axis*, 65kg; nilgai *Boselaphus tragocamelus*, 195kg; and gaur *Bos gaurus*, 730kg; see Table 1.1). The correlation, regression, and ANOVA analyses were done using the statistical package SPSS (*v*.15).

Ordination techniques were used to compare similarities between herbivore species distributions and PAM and PAN in the context of the biogeographic zones. Preliminary analyses using Detrended Correspondence Analysis (DCA) showed that the length of the gradient of the first axis exceeded four standard deviations of the data. Consequently, we chose to analyze data using Correspondence Analysis (CA) rather than a Principal Component Analysis (PCA) since a CA accounts for a greater range of the environmental parameter gradients (Ter Braak, 1995).

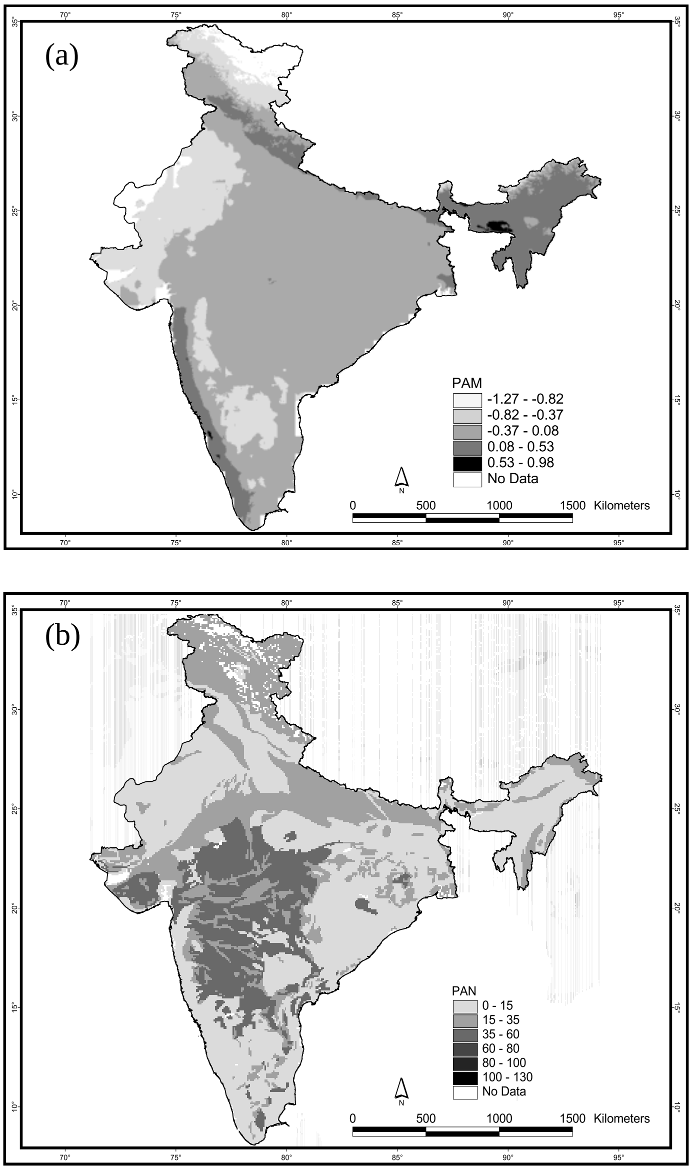


Fig. 7.2. The distribution of (a) plant available moisture (PAM) = ^{10}log(rainfall/potential evapotranspiration), and (b) plant available nutrients (PAN) = cation exchange capacity ($\mathrm{cmol_c\ kg^{-1}}$), in India.

Results

Herbivore species diversity was found to be the highest in areas with high levels of PAN and intermediate levels of PAM (Fig. 7.3). This diversity significantly correlated to PAM ($r = 0.58$, $p < 0.01$) and to a lesser degree to PAN ($r = 0.23$, $p < 0.05$). Both the quadratic and linear terms of PAM had a greater effect on diversity than did PAN (Table 7.1). Species diversity showed a unimodal regression relationship with PAM ($R^2 = 0.53$, $p < 0.001$; Fig. 7.4a), and a weak but significant regression linear model explained the relation between herbivore species diversity and PAN ($R^2 = 0.05$, $p < 0.05$; Fig. 7.4b).

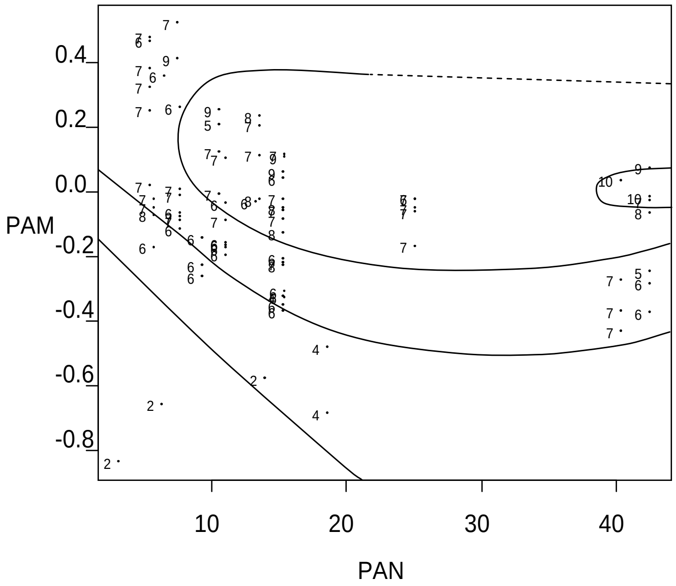


Fig. 7.3. The highest diversity of large mammalian herbivore species occurs in areas of intermediate PAM and high PAN in sub-Himalayan India. PAM (plant available moisture) = ^{10}log(rainfall/potential evapotranspiration); PAN (plant available nutrients) = cation exchange capacity (cmol$_c$ kg^{-1}).

Table 7.1. Results of a ordinary least square multiple regression that describes diversity of 16 large mammalian herbivore species found in 77 Indian protected areas as a function of plant available moisture (linear and quadratic terms) and plant available nutrients.

Coefficient	Regression coefficient	Standard error	t	P
Constant	6.53	0.21	30.67	<0.001
Plant available moisture (linear)	2.79	0.48	5.81	<0.001
Plant available moisture (quadratic)	-4.87	1.03	-4.74	<0.001
Plant available nutrients	0.04	0.01	3.95	<0.001

adjusted $R^2 = 0.59$

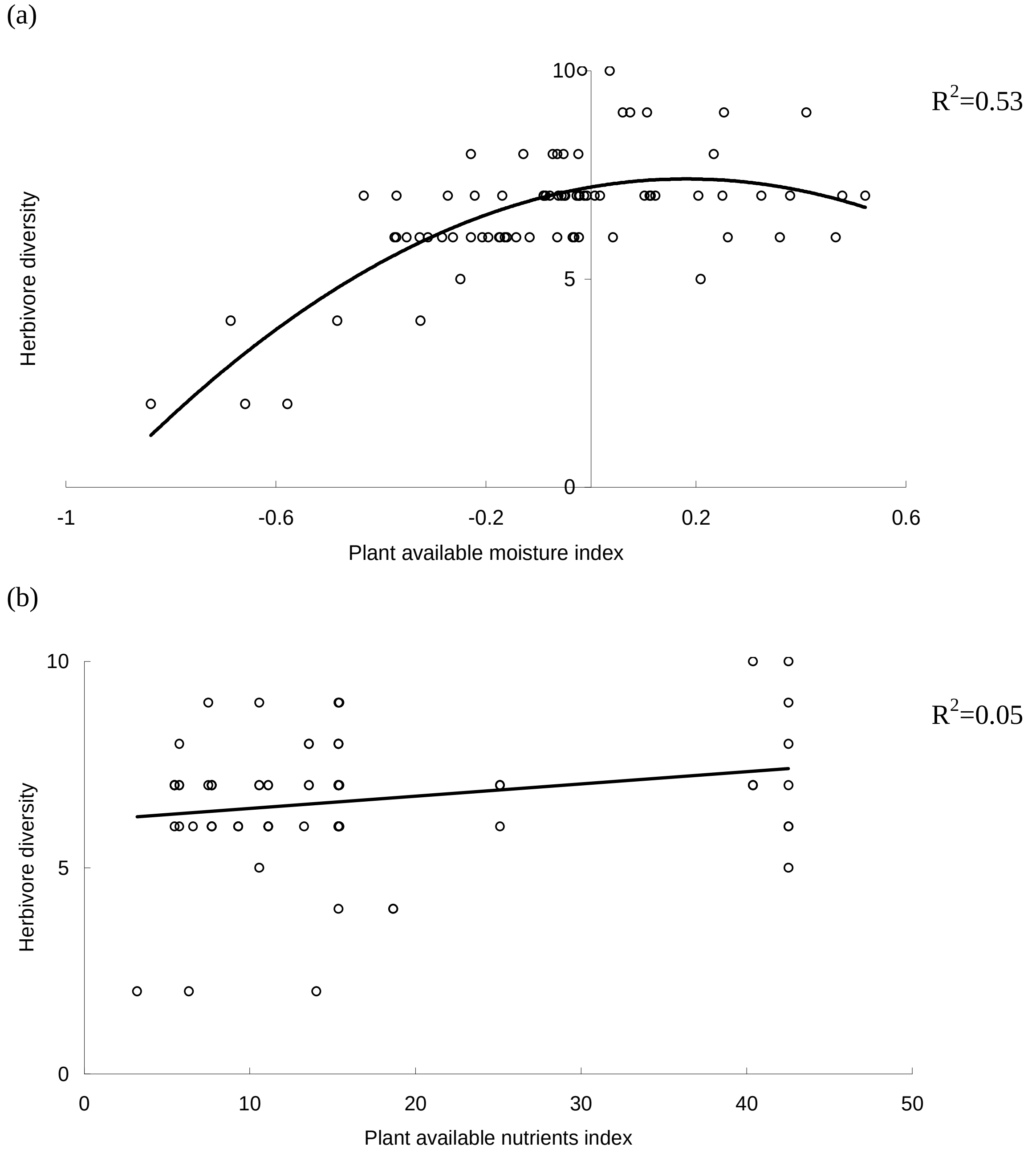


Fig. 7.4. Large mammalian herbivore species diversity found in 77 Indian protected areas along indices of (a) plant available moisture = ^{10}log(rainfall/potential evapotranspiration): $y = -5.92x^2 + 2.16x + 7.21$, $R^2=0.53$, $p < 0.001$; and (b) plant available nutrients = cation exchange capacity (cmol$_c$ kg^{-1}): $y = 0.02x + 6.21$, $R^2=0.05$, $p = 0.04$.

There was a significant effect of PAM on MBM ($F_{(4, 72)}$ = 15.62, $p < 0.001$) explained by a significant positive linear regression model ($F_{(1,72)}$ = 38.61, $p < 0.001$, adjusted R^2=0.41; Fig. 7.5a). A strong effect of PAN on MBM was also found ($F_{(4, 72)}$ = 5.35, $p = 0.001$) explained by a decreasing linear regression model ($F_{(1, 72)}$ = 12.96, $p = 0.001$, adjusted R^2 = 0.16; Fig. 7.5b).

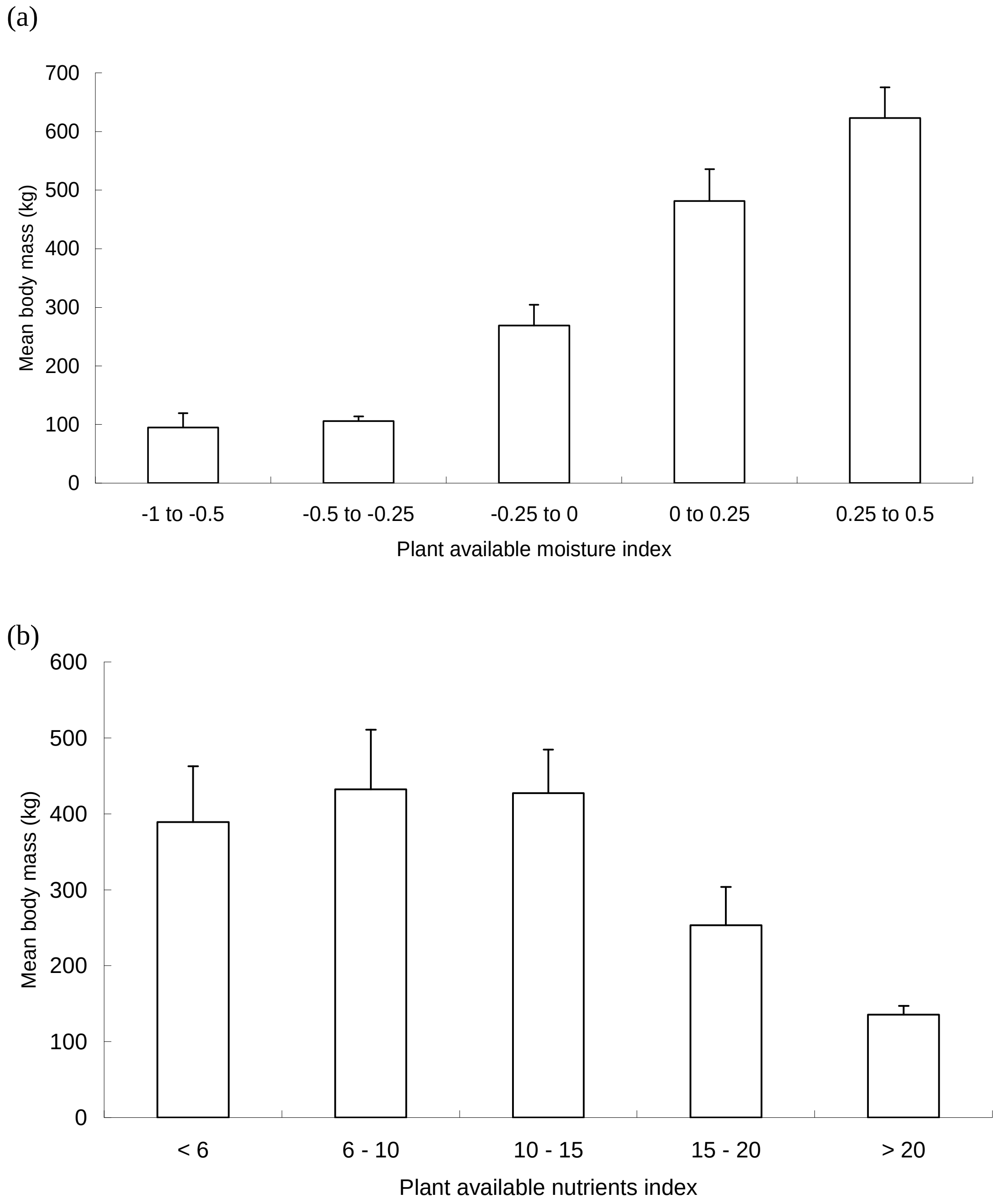
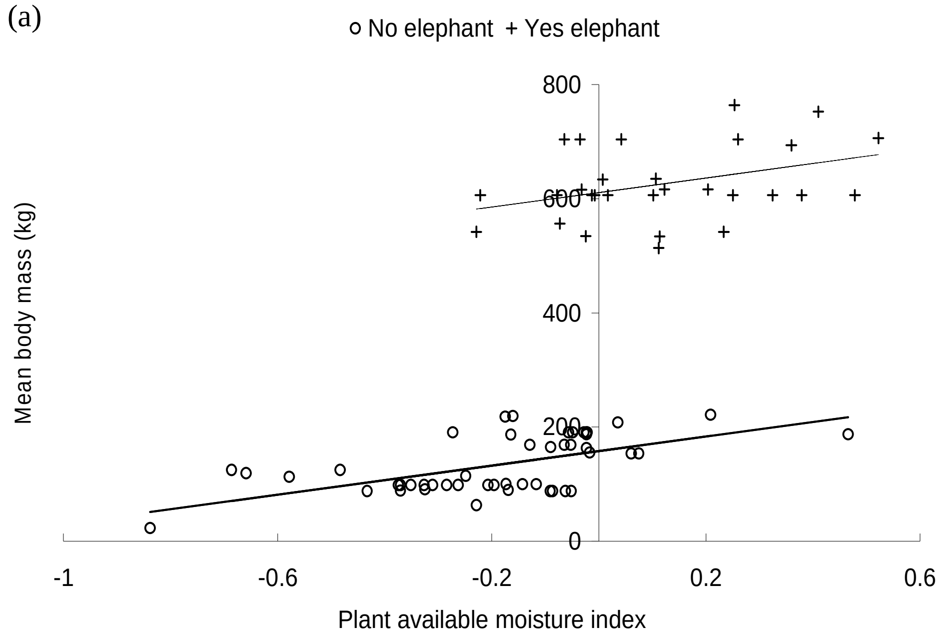


Fig. 7.5. Mean body mass (+ S.E.) of large mammalian species found in 77 Indian protected along indices of (a) plant available moisture = $^{10}\log$ (rainfall/potential evapotranspiration), and (b) plant available nutrients = cation exchange capacity ($\mathrm{cmol_c\ kg^{-1}}$).

The presence of elephants in an area separated the sampled areas into two distinct groups (Figs. 7.6 a,b) and increased adjusted R^2 of the regression model of MBM with respect to PAM to 0.96, but did not alter the fit of the regression model of MBM with respect to PAN.



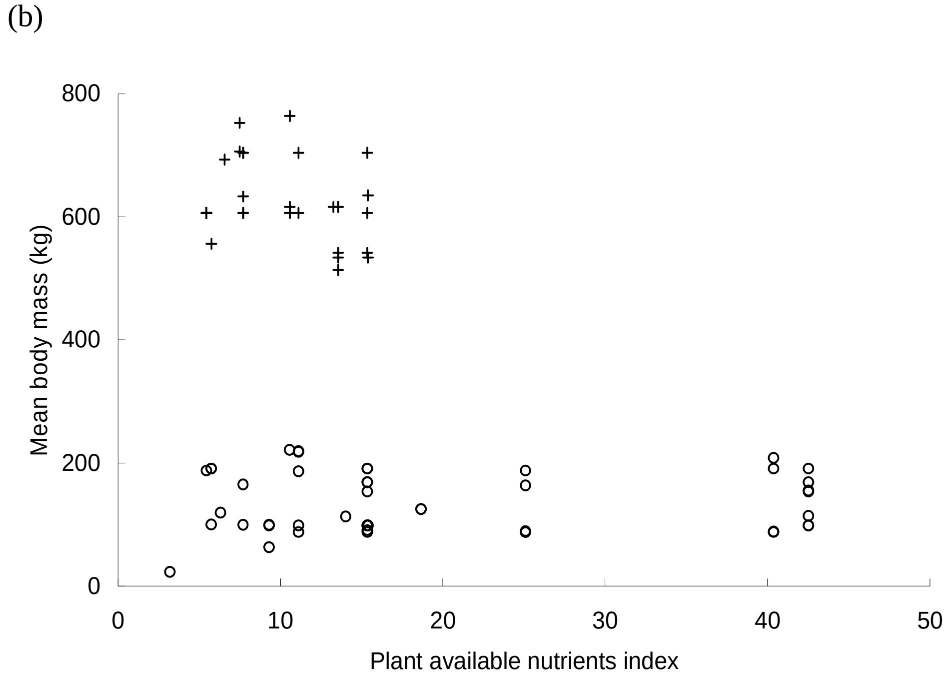


Fig. 7.6. Mean body mass of large mammalian species found in 77 Indian protected areas (o without elephants; + with elephants) along indices of (a) plant available moisture = ^{10}log(rainfall/potential evapotranspiration), (b) plant available nutrients = cation exchange capacity (cmol$_c$ kg^{-1}).

The two largest species, Asian elephant and gaur, were absent from the driest areas, but their frequency of occurrence in the sampled areas increased with increasing PAM and peaked at the highest PAM levels (Fig.7.7a). In contrast the frequency of occurrence of the smallest species, the chinkara, decreased with increasing PAM and chinkara were absent from the wettest areas.

The frequency of occurrence of the largest and smallest species was reversed when they were related to PAN. The frequency of occurrence of Asian elephant and gaur showed a decreasing trend, while that of the chinkara showed an increasing trend with increasing PAN (Fig. 7.7b). The frequency of occurrence of nilgai with respect to PAN mirrored that of chinkara along the same gradient, but at slightly higher frequency levels (Fig. 7.7b).

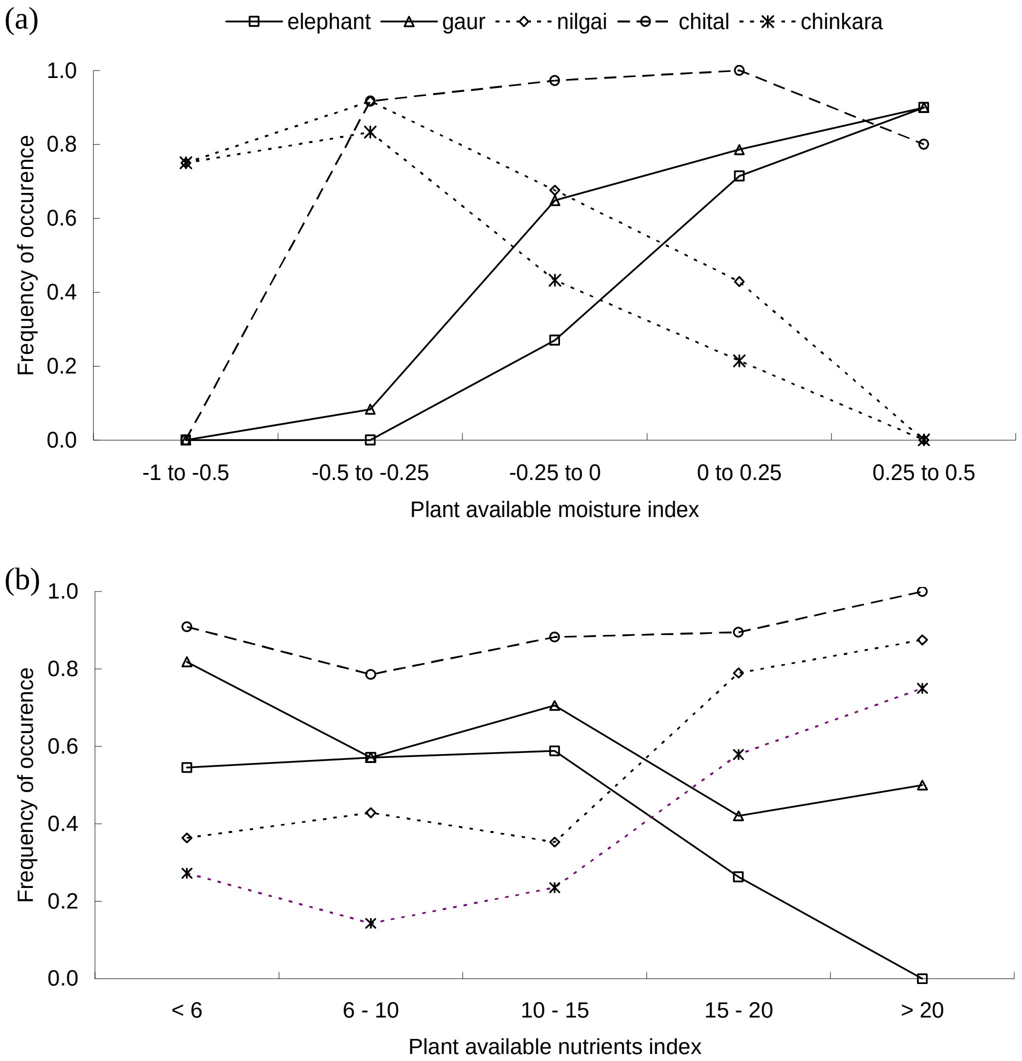


Fig. 7.7. The frequency of occurrence of five herbivore species of differing body mass (Asian elephant *Elephas maximus*, gaur *Bos gaurus*, nilgai *Boselephas tragocamelus*, chital *Axis axis*, and chinkara *Gazella gazelle*) in 77 Indian protected along indices of (a) plant available moisture = ^{10}log(rainfall/potential evapotranspiration), and (b) plant available nutrients = cation exchange capacity (cmol$_c$ kg^{-1}).

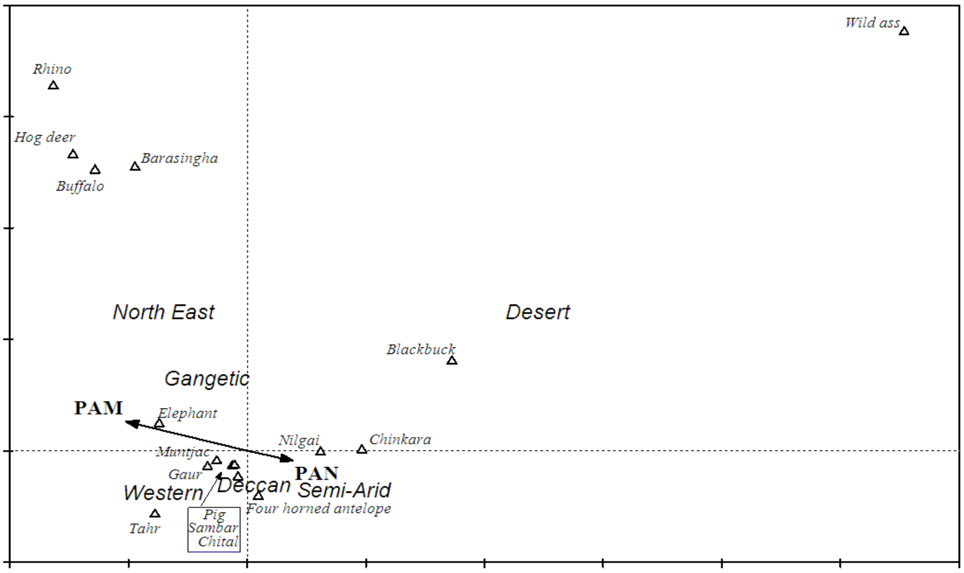


Fig. 7.8. Biplot of Correspondence Analysis (Eigen value of Axis 1=0.4 and Axis 2=0.3) of 16 large mammalian herbivore species distributions found in 77 protected areas located in six biogeographic zones of mainland India - Desert, Semi-Arid, Deccan Plateau, Western Ghats, Gangetic Peninsula, and North-East – in combination with environmental variables PAM (plant available moisture) = ^{10}log(rainfall/potential evapotranspiration), and PAN (plant available nutrients) = cation exchange capacity (cmol$_c$ kg^{-1}).

The Correspondence Analysis results (Fig. 7.8) showed that the ordination values of the antelope (nilgai and four-horned antelope), gazelle (blackbuck and chinkara), and equid species (Indian wild ass) were similar and indicative of areas of high PAN and low PAM (eigenvalues of Axis 1=0.4 and Axis 2=0.3; Fig. 7.8). In contrast, the ordination values of rhino, hog deer, and buffalo were indicative of areas with high PAM; rhino and hog deer are only found in India’s wettest biogeographic zones, the North East and the Gangetic Plain (Fig. 7.8). The ordination values for chital, sambar, and wild pig indicated that they occurred at intermediate levels of both PAM and PAN (Fig. 7.8).

Discussion

The results support the prediction by Olff *et al*. (2002) that areas with high PAN and intermediate PAM should support the highest species diversity. Figure 7.3 shows that the highest large herbivore species diversity in India (10 species) occurs in protected areas in the Deccan Plateau like Kanha and Indravati, areas with high PAN but moderate PAM. The intermediate levels of PAM in the Deccan apparently provide sufficient plant quantity to support the energy requirements of large species like the gaur, while the high PAN levels support the nutrient demands of a number of smaller species like the chinkara, four-horned antelope, muntjac, blackbuck, and chital. The near absence of elephants from the Deccan Peninsula indicates that PAM levels in the Deccan are insufficient to support plant biomass that can satisfy the large absolute energy requirements of elephants.

PAM emerged as a strong predictor of large herbivore species diversity in sub-Himalayan India. This is similar to what has been found in Africa, where rainfall was found to be the dominant predictor of plant biomass and in turn large herbivore species biomass and diversity (Coe *et al*., 1976; East, 1984; Olff *et al*., 2002). In general, the relation between PAN and species diversity in India was weaker than what has been found between PAN and species diversity in Africa (East, 1984; Olff *et al*., 2002). Although it is likely that cation exchange capacity may not completely reflect actual PAN in some areas in India, we did not find a significant correlation with species distribution patterns in India, with either total soil nitrogen (g kg^{-1}) or soil organic carbon content (g C kg^{-1}).

The presence of species with the largest body mass—like elephant, rhino, gaur and buffalo—in areas of low PAN and high PAM, highlight the advantage that their large body mass provides them to tolerate low plant quality (Van Soest, 1982). Smaller species—like the chinkara, blackbuck, and four-horned antelope—were not present in areas with high PAM, likely a result of the nutrient dilution effect in areas with high plant biomass production. Therefore, distribution patterns of species at the extreme ends of the body mass spectrum provide empirical support to validate the body mass-based predictions with respect to both PAM and PAN.

Advantages of larger body mass to tolerate forage of lower quality might explain why the larger nilgai consistently occurred at frequencies higher than that of the smaller chinkara despite distribution patterns of these two species being very similar. The distribution patterns of the nilgai and the chital, however, also demonstrate that not all species in India follow body mass-based principles. The chital is similar in body mass to the Thomson gazelle *Gazella thomsonii*. Yet, the frequency of occurrence of chital is consistently high, in contrast to the low frequency of occurrence of Thomson gazelle in Africa over the same range of PAM values (Olff *et al*., 2002). Although the general patterns of the influence of environmental controls on species diversity still hold, it does suggest that ecological processes at aggregation levels below that of the subcontinent also influence species distribution.

Besides the role of PAM and PAN, anthropogenic practices in India such as man-made fires (Sankaran, 2005), livestock grazing (Madhusudan, 2004), and habitat fragmentation—individually or collectively—might have played a role in shaping structure and availability of plant resources and consequently, herbivores. Klop and Prins (2008) found that fire played a prominent role in determining herbivore species diversity in West Africa. There is also no guarantee that all areas chosen in the analysis had not experienced species extirpations in recent times. However, we took care to include sites that were both large and protected to minimize the extirpation risk. Although there is limited evidence that demonstrates the impact of competition or facilitation within herbivore assemblages, we acknowledge the potential that these ecological forces might have played in shaping herbivore assemblages in India (Arsenault & Owen-Smith, 2002). For example, the analyses by Fritz *et al*. (2002) of herbivore assemblages in Africa in the absence of livestock provides evidence of competition between megaherbivores and smaller herbivore species. If climate change increases PAM as predicted, diversity in areas of low PAN would be expected to increase while diversity in areas of high PAN would be expected to decrease.

In conclusion, this study highlights the strong relation of PAM and herbivore diversity in sub-Himalayan India. Although PAN was found to be a weaker predictor of species diversity, areas with the highest levels of PAN and intermediate levels of PAM support the highest species diversity. This study provides further empirical evidence to support the potential of body mass-resource consumption principles to predict large herbivore species diversity patterns.

Appendix 7.1. The presence (X) of all 16 large (>10kg) mammalian herbivore species found south of the Himalayas in India in 77 protected areas (> 200 km^2) in India's Biogeographic Zones (Rogers & Panwar 1988) excluding the Himalaya, Trans-Himalaya, Coasts, and Islands. PAM=plant available moisture as ^{10}log (rainfall/evaportranspiration); PAN=plant available nutrients measured as cation exchange capacity (cmol$_c$ kg^{-1}); ELP=*Elephas maximus*; RIH=*Rhinoceros unicornis*; GAR=*Bos gaurus*; BUF=*Bubalus arnee*; ASS=*Equus hemionus*; SBR=*Cervus unicolor*; NIL=*Boselaphus tragocamelus*; BAR=*Cervus duvauceli*; THR=*Hemitragus hylocrius*; PIG=*Sus scrofa*; CHT=*Axis axis*; HOG=*Axis porcinus*; BLK=*Antilope cervicapra*; MJK=*Muntiacus muntjak;* FHA=*Tetracerus quadricornis*; CNK=*Gazella bennettii*.

Biogeographic zone	Protected Area	Area (km^2)	ELP	RIH	GAR	BUF	ASS	SBR	NIL	BAR	THR	PIG	CHT	HOG	BLK	MJK	FHA	CNK	PAM	PAN
Indian desert	Desert	860													X			X	-0.67	18.66
	Kachchh Desert	806					X		X						X			X	-0.48	18.66
	Wild Ass	1194					X		X						X			X	-0.84	3.2
Semi-arid	Abohar	357							X						X				-0.35	15.35
	Darrah	893						X	X			X	X					X	-0.59	14.02
	Gir	635						X	X			X	X				X	X	-0.19	11.11
	Kela Devi	879						X	X			X	X				X	X	-0.23	9.3
	Kumbhalgarh	591						X	X			X	X				X	X	-0.05	25.1
	Mount Abu	3568						X	X			X	X				X	X	-0.06	25.1
	Narayan Sarovar	464							X									X	-0.66	6.32
	Ranthambhore	430						X	X			X	X				X	X	-0.21	15.35
	Sariska	500						X	X			X	X				X	X	-0.26	9.3
	Sitamala	640						X	X			X	X				X	X	-0.25	42.52
Western Ghats	Anshi	682	X		X			X				X	X			X	X		-0.31	15.4
	Bandipur	259	X		X			X				X	X			X	X		-0.33	15.4
	Bhadra	1258	X		X			X				X	X			X	X		-0.37	15.35
	Biligiri Rangaswami Temple	551	X		X			X				X	X			X	X		-0.28	42.52
	Dandeli	430	X		X			X				X	X			X	X		0.21	10.57
	Indira Gandhi	558	X		X			X			X	X	X			X	X		0.48	5.45
	Kudremukh	347	X		X			X				X	X			X	X		0.10	11.11
	Mollem	1412			X			X				X	X			X			0.02	5.45
	Mudumalai	7506	X		X			X				X	X		X	X	X		0.32	5.45
	Mundanthurai-Kalakad	765	X		X			X			X	X	X			X	X		-0.22	15.35
	Nagarahole	4953	X		X			X				X	X			X	X		0.25	5.45
	Parambikulam	748	X		X			X			X	X	X			X			0.47	5.45
	Periyar	874	X		X			X			X	X	X			X			-0.01	7.7
	Radhanagari	600	X		X			X				X	X			X	X		0.26	13.56
	Sharavathi Valley	643			X			X				X	X			X	X		0.12	10.57
	Shettihalli	492	X		X			X				X	X			X	X		0.20	13.56
	Srivilliputhur	350	X					X			X	X	X			X	X		0.24	5.45
	Wayanad	539	X		X			X				X	X			X			0.38	5.45
Deccan Peninsula	Achanakmar	500			X			X	X			X	X			X	X		-0.02	13.56
	Andhari	431			X			X	X			X	X			X	X		0.23	13.56
	Bagdara	395						X	X			X	X		X			X	-0.23	15.35
	Bandhavgarh	1127			X			X	X			X	X			X	X	X	0.11	13.56

	Bhimbandh	285						X	X			X	X			X	X		-0.17	25.1
	Bori	345			X			X	X			X	X			X	X	X	-0.27	40.38
	Eturnagaram	437			X			X	X			X	X			X	X		-0.43	40.38
	Gandhi Sagar	940							X			X			X	X	X	X	-0.32	15.35
	Gautam Budha	346						X	X			X	X			X	X		-0.16	11.11
	Gundla Brahmeswaram	542						X	X			X	X			X	X	X	-0.16	11.11
	Gugamal	292			X			X				X	X			X	X		-0.17	11.11
	Indravati	2004			X	X		X	X			X	X		X	X	X	X	-0.09	7.7
	Kanha	585			X			X	X	X		X	X		X	X	X	X	-0.37	40.38
	Kaundinya	478	X					X				X	X				X		-0.37	42.52
	Kawal	482			X			X	X			X	X			X			-0.14	9.3
	Kinnerasani	368			X			X				X	X				X	X	0.04	40.38
	Kotgarh	416	X		X			X				X	X			X			-0.06	15.35
	Kuldiha	687	X		X			X				X	X			X			-0.05	5.75
	Madhav-Shivpuri	287						X	X			X	X				X	X	-0.02	5.75
	Melghat	362			X			X				X	X			X	X	X	-0.07	5.75
	Nagarjunasagar-Srisailam	509						X	X			X	X		X		X	X	-0.06	42.52
	Pachmarhi	1262			X			X	X			X	X		X	X	X	X	-0.02	42.52
	Pakhal	372			X			X	X			X	X				X		-0.09	11.11
	Palamau (Betla)	625	X		X			X	X			X	X			X		X	-0.13	15.35
	Panna	845						X	X			X	X			X	X	X	-0.09	15.35
	Papikonda	399			X			X				X	X		X	X	X		0.06	15.35
	Pench	272			X			X	X			X	X			X	X	X	-0.17	5.75
	Ratapani	745						X	X			X	X			X	X	X	-0.05	15.35
	Sanjay	500						X	X			X	X			X	X	X	0.07	42.52
	Satkosia	186	X		X			X	X			X	X			X			-0.02	25.1
	Satpura	3162			X			X	X			X	X		X	X	X	X	-0.03	42.52
	Semarsot	392			X			X	X			X	X			X	X		-0.02	25.1
	Simlipal	765	X		X			X				X	X			X	X		-0.02	15.35
	Singhori	266						X	X			X	X			X	X	X	-0.01	10.57
	Sitandi	676			X			X	X			X	X			X	X		-0.06	7.7
	Sri Venkateswara	578						X	X			X	X		X	X	X		0.04	15.35
	Sri Lankamalleswaram	288						X	X			X	X				X	X	0.01	7.7
	Sunabeda	422	X		X			X				X	X			X			-0.04	11.11
	Tadoba	320			X			X	X			X	X			X	X		-0.12	7.7
Gangetic Plain	Buxa	1036	X		X	X		X				X	X	X					0.11	15.4
	Corbett	790	X					X	X			X	X	X		X			-0.03	13.27
	Dudhwa	485	X	X				X	X	X		X	X	X		X			0.11	15.4
	Rajaji	520	X					X	X			X	X			X			0.47	7.49
North East	Dibru-Saikhowa	820	X			X		X				X		X		X			0.25	10.57
	Kaziranga	490	X	X	X	X		X		X		X		X		X			0.41	7.49
	Manas	370	X	X	X	X		X				X	X	X		X			0.36	6.57

8

Body mass and large mammalian herbivore ecology in India – a synthesis

Farshid S. Ahrestani

Introduction

From the time Vesey-Fritzgerald (1960) and Lamprey's (1963) theory of 'ecological separation' was proposed as the explanation for the coexistence of large mammalian herbivore species, it has been recognized that food resource partitioning was its mechanistic explanation. Although Hofmann and Stewart (1972) made a strong case that a species' digestive physiology decides which resources a species consumes, landmark studies by Bell (1970, 1971) and Jarman (1973) established that the different metabolic requirements of species of different body mass enabled large herbivore species to coexist. Even today the Jarman-Bell Principle (Geist, 1974) remains the backbone of understanding large herbivore species distribution, ecology, and biology.

A large body of work has shed further insight into how the Jarman-Bell principle works towards partitioning resource between species in space (Olff *et al*., 2002; Du Toit *et al*., 2003; Fryxell *et al*. 2005; Bailey & Provenza, 2008; Van Langevelde & Prins, 2008) and time (McNaughton & Geogidis, 1986; Owen-Smith 2002). All the above studies—and in general the majority of studies from the tropics that have investigated large herbivore ecology within the context of species body mass—are from Africa.

The factors and mechanisms that shape and regulate the ecology and biology of India's rich and diverse large herbivore species community remain largely unstudied and poorly understood. The difference between Africa and India is highlighted by the fact that he has in Africa alpha large mammalian herbivore species richness is as high as 27 in Serengeti, East Africa and 31 in Kruger National Park (McNaughton, 1985; Prins & Olff, 1998), while in India alpha species richness does not exceed ten (Kanha, Central India); my field study site has a species richness of seven (Fig. 8.1). Although species richness in India (for, e.g., seven in field study area) might be less than a fourth of species richness in areas like Kruger (31 species), the body mass range within each assemblage were similar (Fig. 8.1). This suggests that the impact of some factors with the potential to influence large herbivore ecology in the two regions are similar, while others are not.

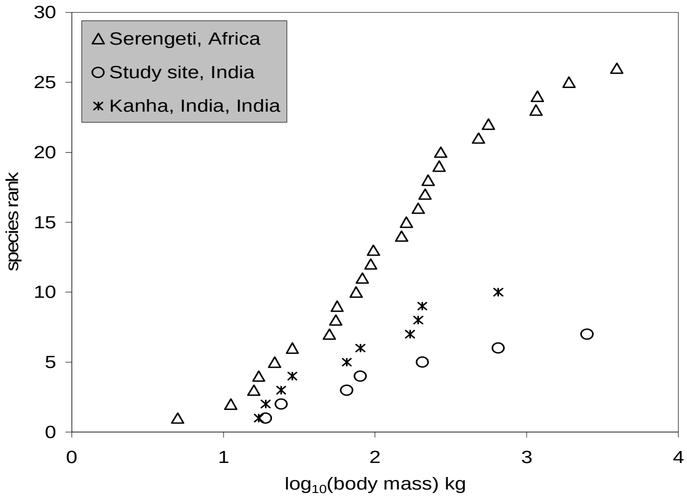


Fig. 8.1. The body mass range and species richness within the large herbivore assemblage in this study's Indian site in comparison to India's and Africa's richest large herbivore species assemblages.

The main goal of this study was, therefore, to understand which factors impact large herbivore ecology and biology in India and how they do so. Within the context of this goal, this study tested different hypotheses—many of them based on body mass based principles, like Jarman-Bell—to help better explain the ecology of large herbivores in India.

Does body mass matter in large mammalian herbivore ecology in India?

The short answer to that question is “yes and no”.

“Yes”

The fundamental premises of this study were that the heterogeneity of food quantity and quality in time and space play a key role in enabling species of different body mass to partition food resources and co-exist, and that the two most important environmental factors that ultimately decide the heterogeneity of plant quantity and quality are the availability of moisture and soil nutrients. Based on these two premises, this study succeeded in finding evidence to show that body mass based theory helps understand large herbivore foraging ecology, *life history* and reproductive biology, and species distribution along spatial, temporal, and organizational scales in India (Fig. 8.2).

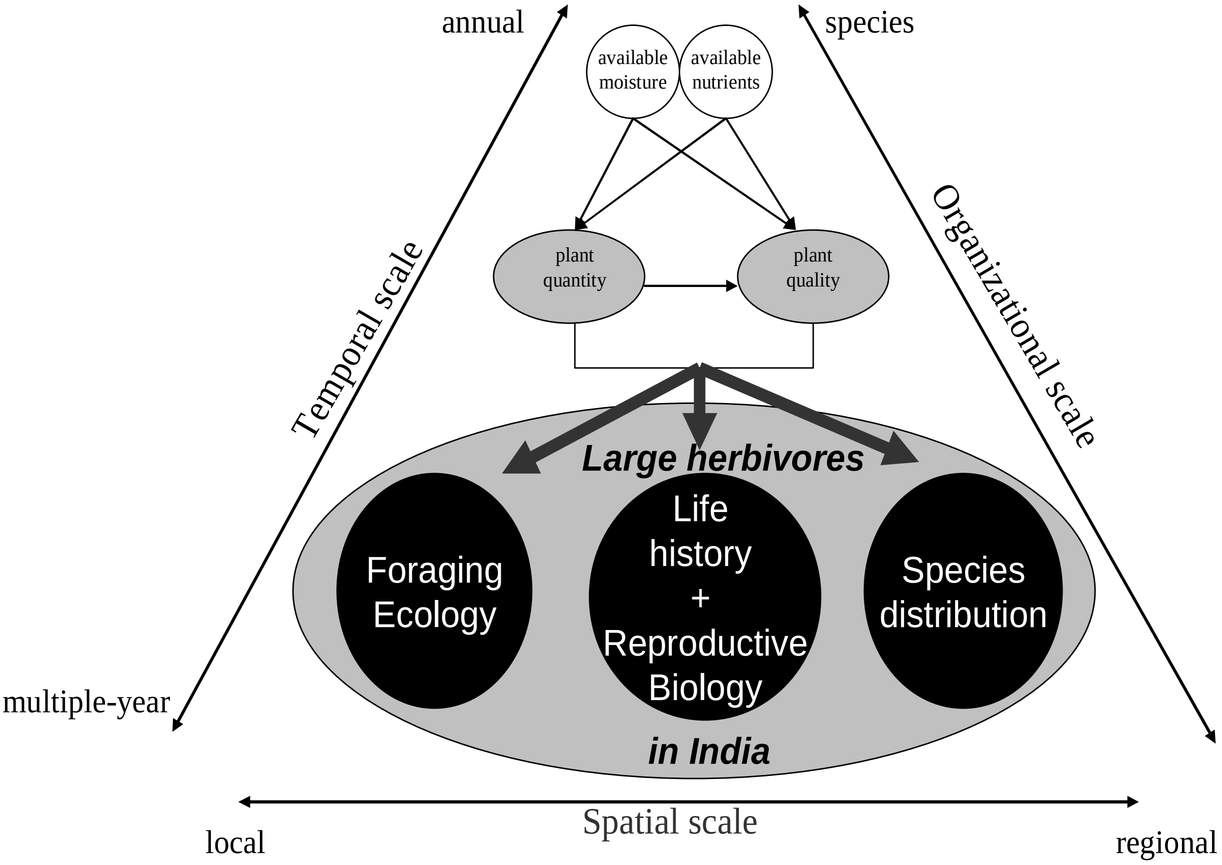


Fig. 8.2. The overall scope of this study: large mammalian herbivore ecology in India with the context of underling environmental parameters.

Along the spatial scale, this study showed that at a country-wide level (Chapter 6) the combination of available moisture and soil nutrients does help explain large herbivore species distributions in India. In general the power of available moisture to predict large herbivore species distribution at the country-wide level scale (Chapter 7) was high and was supported at the local spatial level by the observation that the movement of the large species, like gaur and elephant, appeared to track the seasonal variation in moisture availability in the field study site (Chapter 2).

Also, the high overlap of the distributions of elephant and gaur at the country-level (Chapter 7) was supported by a high 'niche overlap' between these two species at the local level (Chapter 3). Both these species are large, which means that they both require large quantities of food resources. Therefore, although the habitat preference of the two species overlapped, these species differed in digestive physiologies and diet—the gaur is a ruminant species and grazer, while the elephant is a hindgut fermenter and mixed feeder—which offered one explanation for how these large body size species manage to coexist despite high overlap at both the local and regional spatial scales.

Further examination of the effect of physical parameters revealed that the impact available moisture might have on fresh graminoid production, especially when this results in the availability of green forage in the dry season, could contribute to the seasonal habitat preference and local movement by large species (like the gaur in Chapter 3). Also, when plant nitrogen levels are found to be low (Chapters 1 and 2)—and nitrogen is shown to be a limiting factor of graminoid production (Chapter 1)—it normally then follows that soil nitrogen levels are low too (as assumed in Chapter 6). However, soil nitrogen levels in our study site were similar to those found in the Serengeti (McNaughton, 1985). Given that Chapter 1 also showed that rainfall and biomass production levels in both India and Africa were similar, it is possible then that the difference in plant available moisture or nutrients (PAM and PAN)—unless nutrients like phosphorus, or the stoichiometric ratios of different soil properties, differ between the two regions and limit graminoid production in India—do not explain the difference in species richness and diversity between the two continents. In support of the assumption that PAN does not significantly differ between the two continents, similar to Africa, the highest richness of large herbivore species in India were found in areas with the highest soil nutrients (Chapter 7). This also underlined the potential that soil nutrients have to impact large herbivore ecology in India.

In addition to the importance of the impact of the two most fundamental environmental factors, i.e., available moisture and nutrients, the potential impact that fire has on large herbivore ecology cannot be ignored (Van Langevelde *et al*., 2003; Klop & Prins, 2008). Lack of standardized data prevented me from investigating the impact of fire at the country-wide scale. I did, however, find some evidence for the potential role that the grass regrowth after burns has on the local movement of large herbivore species (Gureja & Owen-Smith, 2002; Tomor & Owen-Smith, 2002). Large parts of the moist deciduous forests in the study area burned during the dry season, temporarily transforming tall-grass habitat dominated by *Themeda cymbaria* to short-grass areas with nutritious fresh flush. This 'new' fresh flush was patchy and of short height (< 10cm) and therefore was more suitable for species with smaller jaw sizes and lower nutritional demands like chital, and less suitable for the larger herbivores like gaur and elephant. Also, among African ungulates Wisley (1996) suggested that preference for burnt grassland decreases with increasing body size. It therefore came as no surprise that chital numbers were high in this region just after the fire season in contrast to low numbers of gaur and elephant.

Progressing one trophic level up from physical environmental variables to primary production variables, the restricted spatial distribution of the smaller chital in comparison to the larger sambar and elephants at the local level offers evidence to support findings from Africa that show smaller ruminant species are less evenly distributed in a local landscape when compared to larger species (Du Toit & Owen-Smith, 1989). With respect to the impact of forage quality, Chapter 4 goes as far as to demonstrate that plant quality has the potential to impact the reproductive biology of a large herbivore species population. Although the 'seasonality' hypothesis is not new and was proposed over two decades ago to explain annual calving trends of large herbivore species (Rutburg, 1987), my proposition of the role of body mass is the first explanation for the observed difference in calving behaviour between different species. As differences in the timing of parturition cycles have been observed in African herbivores too, there is little reason not to believe that my proposition would not hold true in Africa as well.

As highlighted in Chapter 4, it is assumed that the availability of plant quality has a greater impact on smaller body mass species than larger species as a function of the Jarman-Bell principle. It was, therefore, interesting to find chital to be relatively common in the far eastern (driest/poor quality) region during the dry season of the study (Chapter 3), especially in large numbers in the 'grazing lawn' region around the tourist camp of Bandipur. The origin of these 'grazing lawns' is unclear, but they are maintained at a short height (< 10cm) by chital grazing as they are not mowed by humans and the incidence of fire in the lawns isn't high (which could be a function of having low combustive biomass). Grazing lawns are known to provide a constant replenishment of fresh graminoid flush that is facilitated by the constant clipping and addition of nutrients in the forms of faeces and urine from the herbivores using these habitats (McNaughton, 1984; Archibald, 2008). Given the generally low quality of graminoid forage in the study area it is plausible that the grazing lawns act as nutrient hotspots for chital (Grant & Scholes, 2006) and play an important role in keeping chital numbers high in the dry deciduous region throughout the year.

In addition to the presumed high quality forage that they provide for the chital, the lawns with their short grasses also provide habitat that allows small herbivores to detect predators more easily. Also, the close proximity of humans—which appeared not to discourage the presence of chital in the lawns—further reduces the threat of large predators at the grazing lawns. Therefore, it may be hypothesized that not only do the grazing lawns provide chital with desirable forage for the longest period in the year, but that they might be preferred by chital because of the lower predation risk they offer.

Further on the theme of body mass and plant quality, I found at the local level that among the habitat parameters measured in the field (Chapter 2), the proportion of tall grass habitat (*Themeda cymbaria*) use increased with increasing species body mass in the dry season. Chital and sambar are known not to forage on *Themeda cymbaria*, while gaur are known to forage on its leaves and elephants uproot tussocks so as to be able to feed on its basal shoots. *Themeda cymbaria* leaves are very rough and have high cell wall content. The difference in the preference between the larger ruminant (gaur) and the smaller ruminants (chital and sambar) could be a function of the superior ability of larger ruminants to tolerate forage of high fibre content.

Although all the above evidence pertains to inter-species comparisons, my study of world's largest Bovini species provided evidence for body mass based ecological separation within a species population. Adult gaur males were often found foraging away from mixes herds of female and juvenile gaur; in the dry season solitary adult males were found foraging in the low quality dry deciduous region more than the females. A review of 40 large herbivore species (Mysterud, 2000) found increasing ecological segregation between the sexes in species with increasing sexual dimorphism; often the larger males were found in habitats of lower quality than those occupied by herds of relatively smaller females.

Body mass has also been linked to sexual dimorphism in species too; sexual size dimorphism has been shown to increase with body mass among species where large males are the larger sex (Fairbairn, 1997; Loison *et al*., 1999). In general, the high sexual size dimorphism in ungulates of large body mass, like the gaur, is understood to have evolved in response to increased polygyny. This increased polygyny in turn is understood to have evolved in their mating system after large herbivores moved from closed-habitat dwellings to open-habitat dwellings (Jarman 1973; Loison *et al*., 1999; Mysterud 2000; Perez-Barberia *et al*., 2002). Gaur are polygynous species, but they are currently found mostly in closed-habitats. It has been argued, however, that the current distribution of gaur in closed-habitats can be misleading as the majority of former open-habitat in regions like India have been lost to the spread of agriculture (Schaller, 1967).

"No"

Although there is evidence to show that body mass based theory can help explain large herbivore ecology in India, it has to be understood that not all large herbivore ecology in India can be explained on only body mass based principles. One prime example was the wide distribution of chital and sambar (Chapter 2) in India that defied explanation of body mass based principles. These species are ubiquitously found in India and are found in areas over a larger gradient of available moisture and soil nutrients. Also, the selection of a primarily browse diet by sambar, a species larger than the chital (which is primarily a grazer), cannot be explained by body mass based principles either. Given the inability of body mass theory to explain sambar's browse diet or wide 'niche breadth', it is tempting to refer back to Hofmann and Stewart (1972) hypothesis that a species digestive physiology might best explain the feeding strategy of some species.

Also, the restricted spatial distribution and narrow 'niche breadth' of the larger gaur being lower than that of the smaller chital and sambar contradicted the understanding that larger species are more evenly distributed in a landscape. Finding the gaur population to have a narrow niche breadth was unexpected, especially given their large body mass. Furthermore, this finding with respect to gaur differed from what we know about the spatial distribution of African buffalo (*Syncerus caffer*) (Prins, 1997), despite the two species being phylogenetically related, and that Chapters 3 and 6 showed that both species have similar *life history* characteristics and diets. One plausible explanation for the restricted 'niche' of gaur was that the large expanse of graminoid biomass in the dry deciduous region during the wet season was optimal forage for gaur to satisfy not only their metabolic requirements at that time but also to build up reserves for the upcoming lean dry season. Therefore, the above findings highlight not only that there exists differences exist between similarly body mass and phylogenetically related African and Indian herbivore species, it also highlights that body mass based principles and conventional understanding of large herbivore ecology need further research.

Another inter-species comparison that cannot be explained by body mass based principles is the fact that despite nilgai (*Boselephas tragocamelus*) being ten times heavier than chinkara (*Gazella bennettii*), the distribution patterns of the two species over country-wide moisture and nutrient availability gradients are near identical (Fig. 7.7a., Chapter 7). While the Nilgai is found in a few areas that chinkara are not, the 10x difference in body mass suggests that there should be a greater difference in their frequency distributions. These findings are, however, similar to high 'niche overlap' that has been found between these nilgai and chinkara in much drier habitat in North India (Bagchi *et al*., 2003)

The impact of large herbivores on their environment

Complementary to the main focus of this study, in which I was trying to discover whether body mass based principles could indeed explain coexistence between larger herbivore species in India, would be a study that tried to understand the potential impact that large herbivores might have on their environment. Studies in Africa have found that herbivores can affect plants (Hawkes & Sullivan, 2001) in many ways including plant community structure (Proulx & Mazumder, 1998; Clay *et al*., 2005; Towne *et al*., 2005), plant spatial heterogeneity (Adler *et al*., 2001), and plant fitness (Wise & Abrahamson, 2005); the availability of nutrients (Bakker *et al*., 2004; McNeil & Hall, 2005); and woody encroachment of savannas (Hagenah *et al*., 2009).

Fig. 8.3. illustrates that the protein content in the leaves from grazed patches in the field study area (Chapter 3) were higher than the nitrogen found in the ungrazed enclosures in our field experiment (Chapter 2) (both areas received similar rainfall and had similar soil nitrogen levels). This, therefore, hints at the possibility of herbivory enhancing nutrient recycling—and in turn enhancing vegetation production—which has ramifications at the study site as well at a larger landscape level. Given that in India the impact of large herbivores on their environment remains poorly unstudied, Fig. 8.3 indicates that field of research deserves attention.

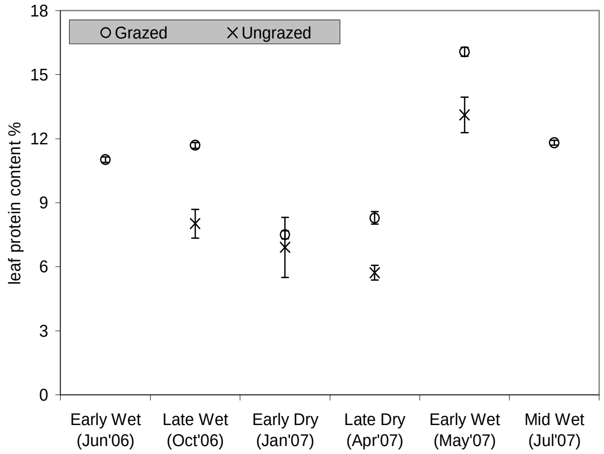


Fig. 8.3. Higher nitrogen content in graminoid leaves that were grazed in the forest in contrast to the ungrazed gramionoid leaves with the experimental plot.

Future challenges

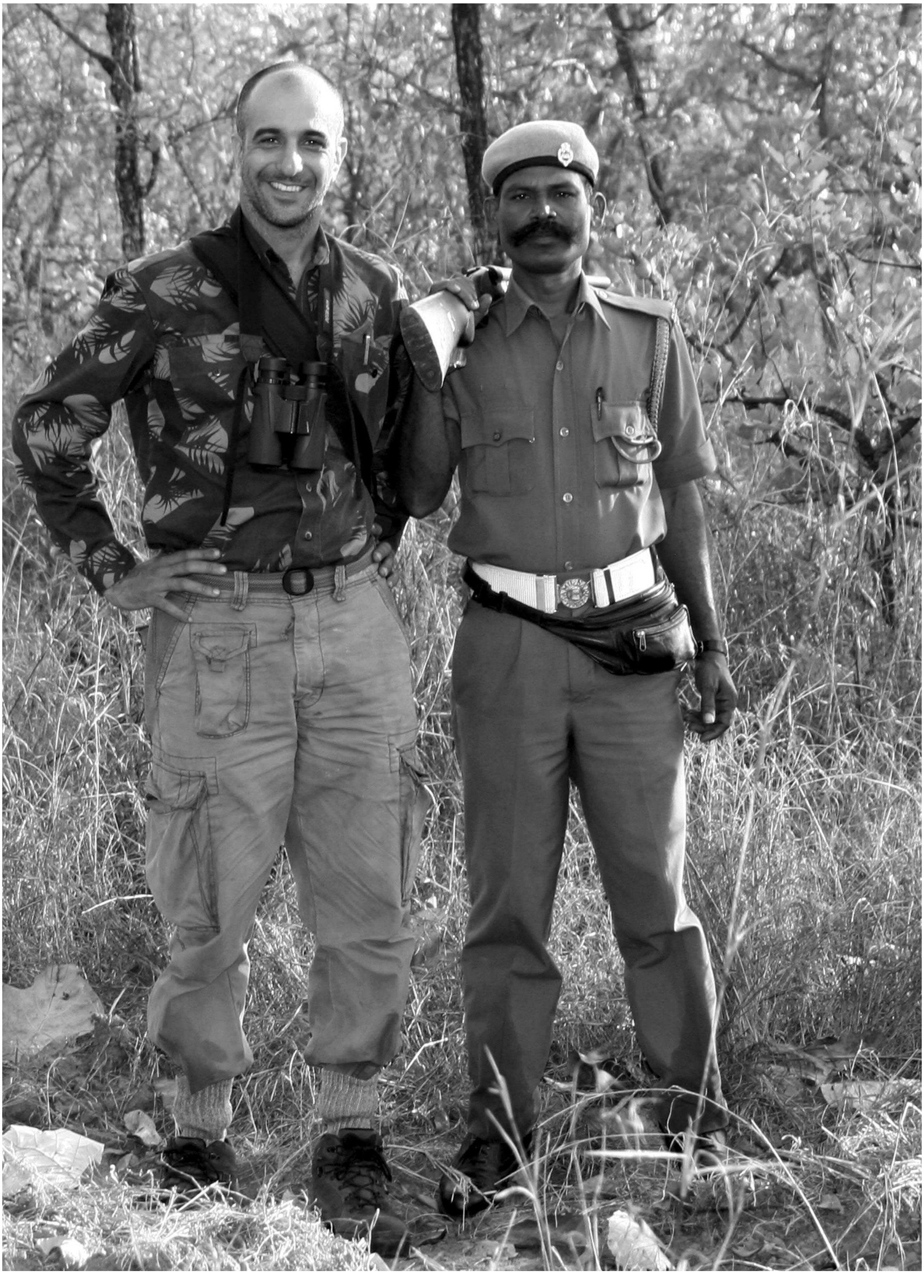
There are many questions that remain unanswered at the end of my study, such as "what are the ecological forces that shaped species richness in Africa so it is four times higher than what is found in India?" Many areas in India support assemblages that range in body mass similar to the body mass range found in areas in Africa that have 4x higher species richness. However, in India there are usually not more than one species representative for a genus, while in Africa there often are multiple species of a genus within the same assemblage. Given that large herbivores species like Bovinae originated in the steppes of Central Asia, why is it that species richness in India is sometimes 25% of what is found in Africa? Answers to these questions can only be found within the context of thoroughly evaluating the differences in the historical and evolutionary changes that have occurred in both areas.

The large herbivore assemblage in India is also different from Africa's because India has multiple Cervid species within its large herbivores assemblage. Correspondence Analysis of species distribution at country level (Chapter 7) shows that antelope and gazelle species in India are found in areas of low PAM and high PAN, while Cervid species like chital and sambar are found in areas that span a large range of PAM and PAN. There are few regions in the world that present the opportunity to study multiple species of both Cervid and Bovid species in the same area. Africa, with the world's richest herbivore assemblage of over 90 species, has only one Cervid species (atlas deer *Cervus elaphus barbarus*) found in the extreme north of the continent (Dorst & Dandelot, 1970), and is not one of them. Other tropical areas like Central and South America have a limited number of large herbivores. Given that India is the last stronghold of most large herbivores in Asia, in addition to having the most diverse assemblage of large herbivores in Asia which includes a mix of both Cervids and Bovids, the large herbivore assemblage in India represents a legitimate alternative to Africa for studying large herbivore ecology in general and an ideal case study to investigate the underlying mechanisms that govern resource partitioning between Cervid and Bovid species of varying body mass.

Looking beyond the differences between India and Africa, the lack of significant correlation of the habitat parameters measured during the local study of species habitat preference demonstrated that either herbivore species were not selecting habitats based on those variables, or that the variables were measured at a scale that was too coarse. Besides the vital importance of the fundamental vegetation parameters such as nutrients, fibre, and lignin content, other vegetation 'quality' parameters like sward height, leaf:stem ratio, and sward bulk density have been shown to influence forage selection by large herbivores (Voeten & Prins, 1999; Drescher *et al.*, 2006 a,b). It follows, therefore, that it might be beneficial to investigate whether these parameters play an equally important role in India as they have been shown to in Africa. While it is possible that some of these parameters will correlate with species habitat and diet selection in India—and shed further insight on how species of different body mass partition resources in India—there may be a need to look at a completely different set of habitat parameters as much of the habitat that remains for India's large herbivore assemblage is forested.

Forested habitat in India is different from the open sparsely wooded savanna landscape in Africa from which much of the understanding of large herbivore ecology has emerged. In general, resources in forested habitats are found more patchily than in open savanna habitats. It is, therefore, perhaps the case that the paradigm "spatial patchiness of available herbaceous forage enables species of different body to partition resources and therefore co-exist", which a lot of recent research on large herbivore community ecology from Africa has focused on and found to be important (Fryxell *et al*. 2005; Cromsigt & Olff, 2006; Prins & Langevelde, 2008), would be deemed important in India as well.

In addition to trying to understand historical reasons like the role that past ecological variation might have played in shaping a region's soil fertility (Schluter & Ricklefs, 1993) and thus eventually its large herbivore species richness and diversity, there is now an immediate need to understand large herbivore ecology in India before it is too late. India's landscape has changed, probably irreversibly, over the last 50 years and today less than 5% of its landscape is available as natural habitat for large herbivore species. Stated earlier, India is the last stronghold for all large herbivores that have a South-Southeast Asian range. Therefore it is imperative that we understand the ecology of these species before we reach a time when we need to manage habitat for the long-term conservation of these species. While much of India’s wildlife landscape has shrunk due to human activity, the continuing rapid spread of dominant invasive species like *Lantana sp*. and *Chromolaena sp*. in wildlife habitats does not bode well for the long-term survival of large herbivores in India either. This underlines the immediate need for more studies at the species as well community scale, local as well as a country-wide spatial scale and short-term as well as long-term scales. Individual as well as multi-collaborative studies of large herbivore ecology are also necessary in India.



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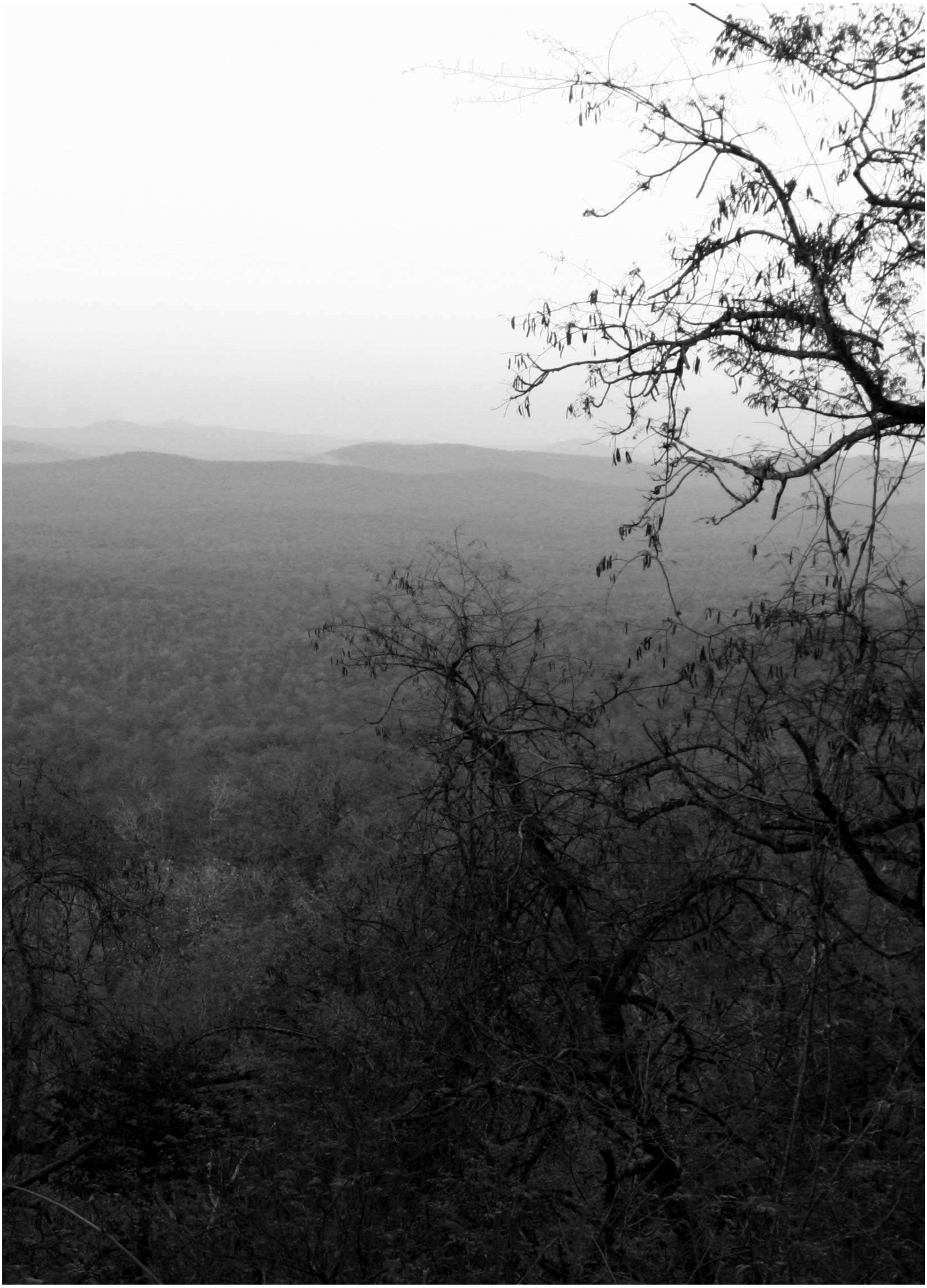

Summary

The study was based on the following premises: That body mass plays an integral role in large herbivore biology and ecology; and that the heterogeneity of food quantity and quality in time and space play a key role in enabling species of different body mass to partition food resources and co-exist; and that the two most important environmental factors that ultimately decide the heterogeneity of plant quantity and quality are the availability of moisture and soil nutrients.

Based on the above premises, this study was intended to shed light on whether body mass based mechanisms could explain large herbivore biology and ecology in India. In short, this study did manage to provide empirical evidence to support the power of body mass based theory—like the Jarman-Bell principle—to explain large herbivore ecology and biology in India across a temporal scale (annual: Chapter 3; multiple year: Chapters 4 & 6), a spatial scale (local: Chapters 3 & 4; regional: Chapters 6 & 7), and a biological scale (species level: Chapters 5 & 6; assemblage level: Chapters 3, 4 & 7). In addition, this thesis improved our understanding of the impact of environmental factors that limit graminoid growth in South India (Chapter 2),

The field-based experiment that I conducted to determine what limits graminoid production in South India (Chapter 2) showed that plant production was limited by nitrogen and not by moisture (despite below average rainfall). Both biomass production and nutrient (nitrogen) content in leaves responded positively to additional nitrogen, but not to additional moisture. I also found evidence that grazing can lengthen the growing period of graminoids in the area. Biomass levels were similar to biomass levels in Africa, but were lower than those found in North India. Leaf nutrient (nitrogen) levels were low when compared to other tropical areas in Africa and Asia. The low nitrogen and high fibre content levels in the dry season would impact the ecology and biology of most large mammalian herbivore species in South India, but the impact would increase with decreasing body mass as a consequence of the Jarman-Bell principle.

At the local spatial scale (Mudumalai and Bandipur Tiger Reserves, South India) using a field based study (Chapter 3) I investigated large herbivore foraging ecology by comparing the seasonal variation of the diet composition, ‘niche breadth’, and ‘niche overlap’ between three ruminant species of varying body mass: chital *Axis axis*, sambar *Cervus unicolor*, gaur *Bos gaurus*, and a mega-hindgut fermenter species, Asian elephant *Elephas maximus*. I found evidence to support my prediction that the smaller ruminant chital, and not the larger ruminants sambar and gaur, would decrease their consumption of graze in the dry season. Gaur were found to be grazers, and sambar browsers, throughout the year. The ‘niche breadth’ of gaur was the least among the species and they showed a preference for the moist deciduous region in the dry season and a preference for the dry deciduous region in the wet season. Also as predicted, elephant had the widest ‘niche breadth’ and was a mixed feeder and its overlap was equally high with that of the other ruminants irrespective of seasons. Body mass theory, therefore, could explain chital and elephant diet and habitat selection, but could not explain the seasonal selection of the habitat and diet selection by sambar and gaur.

In Chapter 4, I proposed that the difference in the impact of body mass on the forage requirements of chital and gaur, particularly lactating females, offers an explanation as to why chital calve at the same time annually and gaur do not. Using a modelling approach, I demonstrated that plant nitrogen content can be a seasonally limiting factor for smaller species like chital but not for larger species like gaur. Also, the extended parturition period of chital implies low synchrony and suggests that predation is not a significant driving factor of the annual timing of chital calving in the study area.

In addition to my investigation of the impact of body mass on a species reproductive biology (Chapter 4), in Chapter 6 I investigated whether the *life history* traits of Asia's largest Bovini species were typical of animals with large body size. Little was known about gaur *life history*, a vulnerable species threatened with extirpation in much of its Southeast Asian range. I developed what is the first reliable methodology to age and sex gaur based on a study of the captive gaur population in Mysore Zoo, South India. Using this knowledge I conducted an 18 month field based study and quantified age and sex structure of the gaur population in my study area. I used supplementary captive gaur data from Mysore Zoo, India's largest captive population, and the world's largest captive population at Omaha Zoo. As predicted, *life history* traits of gaur were of the slow pattern: they sexually mature late (three years for females, four to five for males); they are capable of one birth/year under captive conditions, though in the wild it is probably higher; female-biased adult sex ratio (adult females were three times more abundant than adult males); and their longevity is 20-25 years in captivity, but probably lower in the wild.

Investigating the predictive power of body mass theory at a country-wide level (Chapter 7), I analyzed the distribution of India's sub-Himalayan 16 species large herbivore assemblage in relation to plant available moisture and nutrients. Plant available moisture emerged as a stronger predictor of herbivore diversity in Sub-Himalayan India than plant available nutrients. As predicted, herbivore diversity was highest in areas with high levels of soil nutrients and intermediate levels of available moisture. Intermediate levels of available moisture support sufficient plant biomass to support the energy requirements of intermediate and large body mass herbivores, and high levels of nutrients ensure both higher quantity for larger species and higher plant quality for smaller species. Large body mass species were present in areas of low available nutrients but high available moisture, which supports the hypothesis that large herbivore species are capable of surviving in areas with low plant quality that might not support herbivores of smaller body mass.

Finally, in Chapter 8 I come to the conclusion that some of my results support body mass based theory, while others do not. A good example of this was the contrast between the local distribution of chital and gaur in our study site: the chital's rather uneven distribution in the study area supports findings from Africa that show the smaller species are distributed less evenly over a landscape than larger species; but the narrow and restricted distribution of gaur, a relatively large body mass species, is in contrast to what the expectation of large body mass species being evenly distributed over a local landscape.

In conclusion, this study is the first of its kind to investigate the impact of body mass on large herbivore ecology, biology, and distribution in India across spatial, temporal, and biological scales. It showed that body mass based principles have the potential to explain large herbivore biology and ecology, but at the same time the theory leaves a lot of questions unanswered.

Samenvatting

Dit onderzoek was gebaseerd op de volgende aannames: 1) dat lichaamsgewicht een integrale rol speelt in de biologie en ecologie van grote herbivoren; 2) dat de heterogeniteit van voedselkwantiteit en –kwaliteit op verschillende temporele en ruimtelijke niveaus een centrale rol speelt in het in staat stellen van soorten met verschillend lichaamsgewicht om samen te leven en voedselbronnen te verdelen; 3) dat de twee belangrijkste omgevingsfactoren die de heterogeniteit van plantkwantiteit en –kwaliteit beïnvloeden de beschikbaarheid van vocht en nutriënten in de bodem zijn.

Dit onderzoek was bedoeld om, op basis van eerder genoemde aannames, duidelijk te krijgen of mechanismen gebaseerd op lichaamsgewicht de biologie en ecologie van grote herbivoren in India verklaren. Samenvattend, dit onderzoek geeft het empirische bewijs om de op lichaamsgrootte gebaseerde theorie—zoals het Jarman-Bell principe—te ondersteunen en zo de biologie en ecologie van grote herbivoren in India over een temporele schaal (jaarlijks: hoofdstuk 3; meerdere jaren: hoofdstukken 5 & 6), ruimtelijke schaal (lokaal: hoofdstukken 3 & 4; regionaal: hoofdstukken 5 & 6) en biologisch organisatieniveau (soortniveau: hoofdstuk 5; assemblageniveau: hoofdstukken 2, 3 & 6) te verklaren. Daarnaast verbetert dit proefschrift ons begrip van de omgevingsfactoren die de groei van grassen in Zuid-India beperken.

Het veldexperiment dat ik heb uitgevoerd om te bepalen wat de productie van grassen beperkt in Zuid-India toont aan dat deze productie beperkt werd door stikstof en niet door water (ondanks lagere regenval dan gemiddeld). Zowel de productie van biomassa als de hoeveelheid nutriënten (stikstof) in de bladeren reageerden positief op toevoeging van stikstof, maar niet op toevoeging van water. Ik heb ook ontdekt dat begrazing de groeiperiode van grassen in dit gebied kan verlengen. De hoeveelheid biomassa was gelijk aan die in Afrika, maar was lager dan die in Noord-India. De hoeveelheid nutriënten (stikstof) in de bladeren was laag vergeleken met andere tropische gebieden in Afrika en Azië. Het lage stikstof- en hoge vezelgehalte in het droge seizoen zou de ecologie en biologie van de meeste plantenetende zoogdieren moeten beïnvloeden, en deze invloed zou, als gevolg van het Jarman-Bell principe, moeten toenemen naarmate het lichaamsgewicht afneemt.

Op het lokale ruimtelijke niveau (Mudumalai en Badipur Tijger Reservaten, Zuid-India) heb ik, door middel van veldwerk, foerageerecologie van grote herbivoren onderzocht door de seizoensvariatie van de dieetsamenstelling, de breedte van de niche, en de overlap tussen niches te vergelijken tussen drie herkauwers met verschillend lichaamsgewicht: chital *Axis axis*, sambar *Cervus unicolor*, gaur *Bos gaurus*, en een dikke-darmverteerder, de Aziatische olifant *Elephas maximus*. Hiermee heb ik bewijs gevonden om mijn voorspelling, dat de kleine herkauwer chital en niet de grotere herkauwers sambar en gaur hun grasconsumptie in het droge seizoen verlagen, te ondersteunen. De gaur bleek het hele jaar door een grazer te zijn, en de sambar het hele jaar door een knabbelaar. De breedte van de niche was het kleinste bij de gaur, welke een voorkeur had voor de natte gebieden in de droge tijd en voor de droge gebieden in de regentijd. De olifant had, ook zoals voorspeld, de breedste niche en had een gemengd dieet, terwijl de overlap (van zijn niche) even hoog was als die van de andere herkauwers, ongeacht het seizoen. De theorie over de invloed van lichaamsgewicht kon dus het dieet en de habitatkeuze van de chital en olifant verklaren, maar kon niet de seizoensafhankelijke keuzes van de gaur en de sambar verklaren.

In hoofdstuk 4 stelde ik dat het verschil in invloed van lichaamsgewicht op voedselbenodigdheden van chital en gaur, met name die van zogende vrouwtjes, verklaart waarom chital jaarlijks gelijktijdig jongen krijgen en gaur niet. Met een modelaanpak liet ik zien dat de hoeveelheid stikstof in planten een beperkende factor kan zijn in sommige seizoenen voor kleinere soorten zoals de chital, maar niet voor grotere soorten zoals de gaur. Daarbij impliceert de verlengde periode van drachtigheid bij chital lage synchronie en suggereert dit dat predatie geen significante rol speelt bij de jaarlijkse timing van het krijgen van kalveren in het studiegebied.

Ter aanvulling op mijn onderzoek naar de invloed van lichaamsgewicht op de voortplantingsbiologie van de soorten (hoofdstuk 5), heb ik in hoofdstuk 6 onderzocht of de *life-history* eigenschappen van Azië's grootste rundersoorten typerend waren voor grote dieren. Er was weinig bekend van de *life-history* van de gaur, een kwetsbare soort die in een groot gedeelte van zijn Zuidoost-Aziatische verspreidingsgebied dreigt uitgeroeid te worden. Ik heb de eerste betrouwbare methode ontwikkeld om de leeftijd en het geslacht te bepalen van de gaur, gebaseerd op het bestuderen van een gevangen populatie in de dierentuin van Mysore, Zuid-India. Met deze kennis heb ik gedurende achttien maanden de leeftijdsopbouw en geslachtssamenstelling van de populatie in mijn studiegebied bepaald. Ik heb aanvullende gegevens gebruikt van gevangen populaties uit de dierentuin van Mysore, de grootste in India, en van 's werelds grootste gevangen populatie uit de dierentuin van Omaha. Zoals verwacht heeft de gaur een langzame levensstijl. Ze worden laat volwassen (na drie jaar voor de vrouwtjes, na vier tot vijf jaar voor mannetjes); ze zijn in staat een jong per jaar te werpen in gevangenschap, hoewel dit in het wild waarschijnlijk meer is; de geslachtsverdeling is in het voordeel van de vrouwtjes (volwassen vrouwtjes kwamen drie keer zo veel voor als volwassen mannetjes); en de levensverwachting is 20-25 jaar in gevangenschap, maar waarschijnlijk is deze korter in het wild.

Om te onderzoeken wat de voorspellende waarde is van de lichaamsgewichttheorie op landelijk niveau, heb ik de verspreiding van de, zestien soorten grote, sub-Himalaya herbivoor assemblage geanalyseerd in relatie tot het voor planten beschikbare water en nutriënten. Het voor planten beschikbare water kwam naar boven als een betere verklaring dan de hoeveelheid beschikbare nutriënten. De diversiteit aan herbivoren was, zoals voorspeld, het hoogst in gebieden met grote hoeveelheden nutriënten in de bodem en gemiddelde hoeveelheden beschikbaar water. Gemiddelde hoeveelheden beschikbaar water voorzien in voldoende plantenbiomassa om de herbivoren met een groot en gemiddeld lichaamsgewicht van energie te voorzien, terwijl de grote hoeveelheden nutriënten zorgen voor zowel hogere kwantiteit aan plantenbiomassa voor de grotere herbivoren als voor hogere kwaliteit van planten voor de kleinere herbivoren. Soorten met een groot lichaamsgewicht waren aanwezig in gebieden met veel beschikbaar water en weinig beschikbare nutriënten, wat de hypothese ondersteunt dat herbivoren met een groot lichaamsgewicht wel in staat zijn te overleven in gebieden met lage voedselkwaliteit en herbivoren met een klein lichaamsgewicht niet.

Tenslotte kom ik in hoofdstuk 7 tot de conclusie dat een deel van mijn resultaten de lichaamsgewichttheorie ondersteunt, terwijl een deel dat niet doet. Een goed voorbeeld hiervan was de tegenstelling tussen de lokale verspreiding van de chital en die van de gaur in het onderzoeksgebied: de meer ongelijke verspreiding van de chital ondersteunt bevindingen uit Afrika, waar kleinere soorten een minder gelijke verspreiding hebben over het landschap dan grotere soorten; maar de ongelijke verspreiding van de gaur, welke een relatief groot lichaamsgewicht heeft, strookt niet met de verwachtingen tegen dat grotere dieren een meer gelijke verspreiding zouden moeten hebben in een landschap.

Dit onderzoek is het eerste in zijn soort dat de invloed van lichaamsgewicht op de ecologie, biologie en verspreiding van grote herbivoren in India onderzoekt op verschillende ruimtelijke, temporele en biologische schaalniveaus. Het laat zien dat de principes van de invloed van lichaamsgewicht de potentie hebben verklaringen te verschaffen voor de ecologie en biologie van grote herbivoren, maar ook dat deze principes veel vragen niet kunnen beantwoorden.

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